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Zoogeography of the treefrogs in Africa's tropical forests

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The zoogeographical patterns of the forest faunas of treefrogs (Hyperoliidae and genus *Leptopelis*) in tropical Africa are analysed. This group is well-suited for such a work since especially the genus *Hyperolius* shows great diversification and signs of recent speciations. For the purpose of this analysis, the species are separated into sylvicolous ("high forest") and parasylvicolous ("farmbush"). The forests in this study are tentatively divided into ten forest blocks based on differences in the treefrog fauna, and such differences are analysed.

The sylvicolous species of the genus *Hyperolius* have a distribution pattern with a total separation at species level between forest blocks which may reflect the division of the forest belt through drier periods of late Pleistocene into a number of isolated refugia where moist forest and its fauna have persisted and may have resulted in allopatric speciation. The genera *Afrixalus* and *Leptopelis* show less diversification since the sylvicolous species of these genera are separated into three regions, or groups of forest blocks, with groups of species common for these regions, but with no species common between these regions, and only slightly overlapping in southern Nigeria. These regions are West Africa west of the Dahomey Gap/Nigeria, Central Africa and the Eastern Forests.

The parasylvicolous species show a fundamentally different distribution pattern. One group is found in West Africa and in Central Africa along the Atlantic coast but not far inland. Another group is found in Central Africa, including Cameroun and easternmost Nigeria and the forest block along the Atlantic coast. Finally one group is widely distributed in the dry parts of the Eastern Forests. The three groups are separated at species level, but the former two have a considerable area of geographical overlap along the Atlantic coast of Central Africa from Cross river southwards. The distribution of the parasylvicolous fauna does not show well-defined "faunal breaks" similar to the sylvicolous fauna, but species diversification and distinction between vicariant taxa seem to have taken place at different, apparently "random" places, perhaps reflecting the original, linear distribution of this fauna in a narrow forest edge towards the savanna.

The ill-delimited orophile treefrog faunas are found in three areas with full separation at species level: Mount Cameroun and the Cameronese ridge; the mountains in Central Africa (Albertine Rift and adjacent highlands); and the Eastern Arc Mountains.

A recent proposal that the species structure in the genus *Hyperolius* can be traced back to Cretaceous is discussed. It is argued that climatic changes in late Pleistocene are sufficient to explain the present species structure.

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Introduction

It can be argued that the exploration of Amphibia in tropical Africa is still so fragmentary that a comprehensive zoogeographical analysis is premature – or that attempts to perform such an analysis, even on an incomplete background, are useful as an inspiration for further studies. Such an attempt is presented here, based on many years of fieldwork in tropical Africa, and on the taxonomical work of many authors (compilation in Schiøtz, 1999).

The aim of the present paper is to analyse the zoogeographical patterns of the forest faunas of treefrogs in tropical Africa. For the analysis, these forest-related faunas are divided into two groups relating to their habitat, generally sympatric but not syntopic, i.e. sylvicolous (high forest) and parasylvicolous (farmbush/bushland) species.

Treefrogs are here defined as the group conventionally termed the family Hyperoliidae, although recent studies (Frost et al., 2006) indicate that the genus *Leptopelis* does not belong in this group (see app. 1). The mainly Asian treefrog family Rhacophoridae has only one forest related member in Africa, *Chiromantis rufescens*, but there is some doubt (Rödel, in litt.) whether populations from western and central Africa are conspecific. This species is therefore not treated further here.

The present attempt to base a zoogeographical treatment on ecological divisions is inspired by studies from West Africa (Schiøtz, 1967) of the three clearly separate lowland faunas, associated with savanna, high forest and farmbush respectively. Among them, especially the latter is sympatric but rarely syntopic with the former two. It was shown in the West African study that these three faunas show three clearly different distribution patterns: the savanna-living species are generally widely distributed throughout the West African savanna and further East, often stretching to western Ethiopia and Uganda, the high forest species are clearly localised to "forest islands", today partly confluent, and the farmbush fauna has a wide distribution, with tendencies to subspecific or specific splitting up at apparently "random" places throughout West Africa.

The paper is an attempt to carry out a similar analysis for the entire forest belt of tropical Africa, and more specifically to address a number of questions, such as: (1) is there a basic difference in the zoogeographical pattern of the two proposed "faunas", sylvicolous and parasylvicolous, making it relevant to analyse the two faunas separately?; (2) what are the zoogeographical patterns for the two faunas?; (3) what is a possible explanation for these patterns?

A problem with the present treatment based on an ecological division is that a direct comparison with Poynton's several papers (e.g. Poynton's 1999 benchmark paper) is difficult, since his approach, without a clear distinction between the faunas, tends to obscure part of what I see as the distinctness of the biogeographical regions and blocks.

The African treefrogs are deemed suitable for such a study because: (1) their distribution is reasonably well known on a continental scale; (2) the taxonomy of the forest-related species is reasonably settled; (3) so are their habitat preferences; (4) they show signs of recent speciation; (5) they contain a sufficiently large number of taxa for analysis.

Source : MNHN, Paris

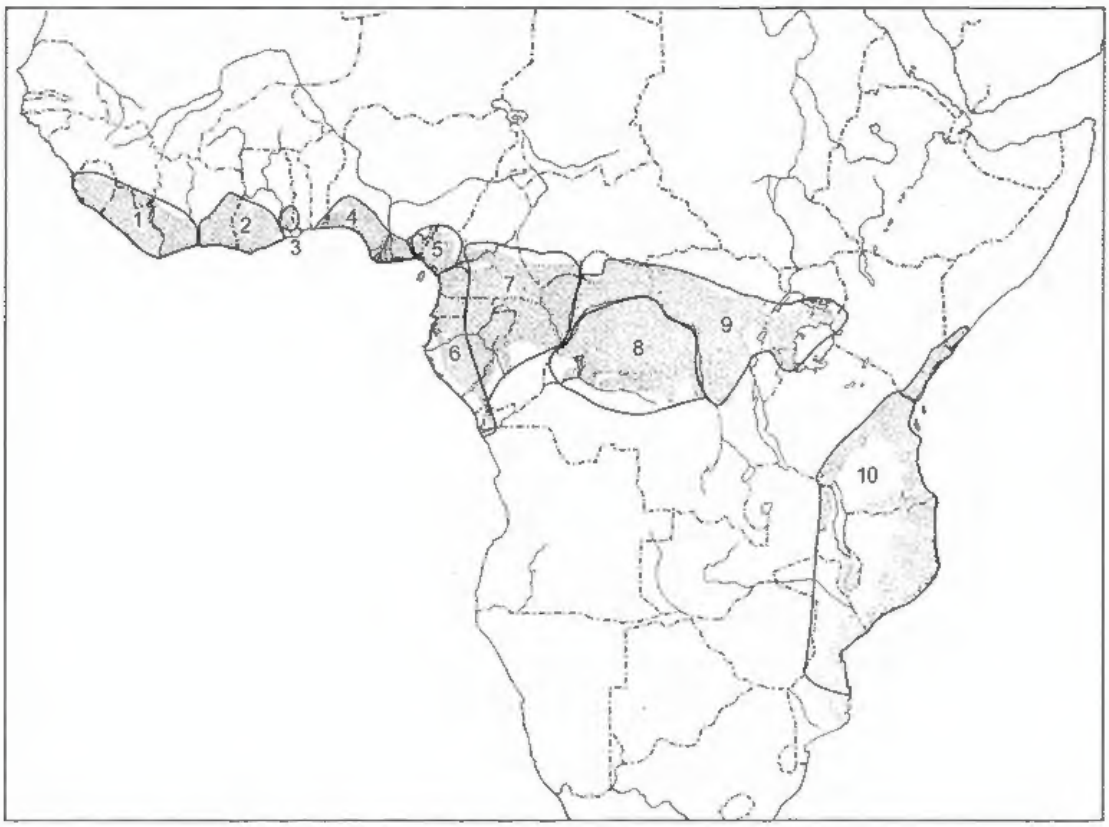


Fig. 1. – Division into forest blocks.

The dotted areas on the map represent for West- and Central Africa moist, evergreen forest (rainforest) as climax vegetation. In Eastern Africa such areas represent rainforest in the Eastern Arc as well as dry, semideciduous forest inhabited by the parasylvicolous fauna.

The numbers refer to forest blocks (see text): 1, Liberia; 2,: Gold Coast; 3, Trans-Volta-Togo; 4, Southern Nigeria; 5, Cross-Sanaga Coastal Forests; 6, Congolian Coastal Forests; 7, North-western Congolian Forests; 8, Central Congolian Forests; 9, North-eastern Congolian Forests; 10, Eastern Forests.

Our knowledge of the distribution of the Amphibia in the forest regions of Africa spreads from very good (Cameroun, western Côte d'Ivoire, Eastern forests) to grossly inadequate (much of the Congo basin).

The taxonomic knowledge of most treefrog genera is fair in the way that they have been subjected to rather recent treatments over large areas – sometimes continent-wide – although it can be argued that a thorough systematical treatment based on DNA, which will give us a deeper understanding of the phylogenetic relationships, has just started, and has until now been so sporadic that the conclusions drawn can be disputed.

The level of knowledge of the two faunas, parasylvicolous and sylvicolous, is very different. The conspicuous and easily accessible parasylvicolous fauna tends to be well-known, whereas the sylvicolous fauna is incompletely known until searched for by experienced collectors, seeking unconventional and sometimes inaccessible places and finding the

Source : MNHN, Paris

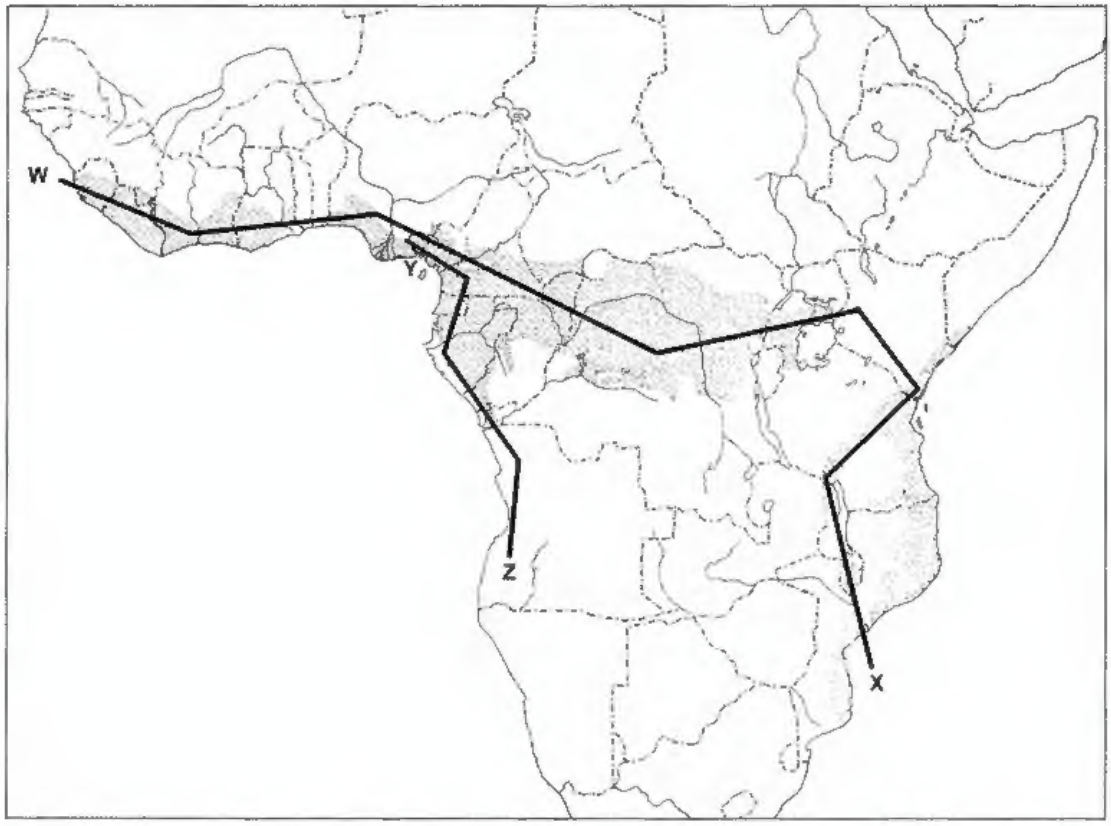


Fig 2. – Transect lines used in tables 1-4.

few and scattered specimens guided by their voices. The rule is therefore that the sylvicolous fauna tends to have been recently described and that new discoveries are mainly made in this group.

Although most taxa treated here are known from a reasonable number of localities, the exact borders of their distribution are often guesswork. For the parasylvicolous fauna, in most cases we have a satisfactory density of records, and furthermore often sets of allopatric taxa – sometimes regarded as subspecies – replacing each other in a way we interpret as vicariance, not only geographically but also ecologically. The sylvicolous fauna is more difficult. A number of species were recorded only from part of the proposed ecoregion. Sometimes it is because only this part has been thoroughly searched, sometimes because the species may be confined to a wetter, "richer" core area. Both explanations seem valid for the rich fauna of western Côte d'Ivoire, the part of the forest block with most rainfall, but also by far the best explored forests in the Liberia block. The richness of the faunas of southern Cameroun compared to areas to the East and South may mainly be due to the thorough collecting effort here. A consequence of this uncertainty – not likely to be solved in the near future – is that whereas the distinction between faunas of the forest blocks can be assessed, the identification of the exact borders between them, especially in Central Africa, must be left open.

Source : MNHN, Paris

Table 1. – Distribution of sylvicolous taxa, from Sierra Leone to the Indian ocean, along transect W-X (fig. 2).

The numbers refer to forest blocks (see text and fig. 1): 1, Liberia; 2,: Gold Coast; 3, Trans-Volta-Togo; D: Dahomey Gap; 4, Southern Nigeria; 5, Cross-Sanaga Coastal Forests; 6, Congolian Coastal Forests; 7, North-western Congolian Forests; 8, Central Congolian Forests; 9, North-eastern Congolian Forests; A, Arid Corridor; 10, Eastern Forests. FN, Footnotes. Note that block 8 breaks the linear sequence. +++, widely distributed within the block; ++, collection effort insufficient to show distribution; +, only known from very restricted range in spite of ample collection; C, Central; E, East; N, North, S, South; W, West. Abbreviations of generic names in this table and next ones: *A*, *Afrixalus*; *Ac*, *Acanthixalus*; *Al*, *Alexteroon*; *Ar*, *Arlequinus*; *C*, *Callixalus*; *Ch*, *Chlorolius*; *Cr*; *Cryptothylax*; *H*, *Hyperolius*; *K*, *Kassina*; *L*, *Leptopelis*; *O*, *Opisthothylax*; *P*, *Phlyctimantis*.

Species name	1	2	3	D	4	5	6	7	8	9	A	10	FN
H. chlorosteus	+++												
H. zonatus	+++												
H. wermuthi	+												
H. nienokouensis	+												
K. lamottei	+												
Ac. sonjae	++	++											
L. macrotis	+++	+++											
A. vibekensis	+	+											
H. viridigulosus	E	+++											
H. laurenti		+++											
H. bobirensis		++											
L. occidentalis	+++	+++			?								1
A. nigeriensis	+++	+++			+++								
H. torrentis			++										
L. brevirostris					++	+++	N						
O. immaculatus					++	+++	N	++					
L. boulengeri					?	+++	++	?	?	?			1-2
Al. jynx						+							
H. bopeleti						S	N						3
A. schneideri						?							
Ar. krebsi						++							
L. modestus						+++							4
Ch. koehleri						+++	N						
H. acutirostris						+++	N						
L. rufus						+++	+++						
H. endjami						+++	+++						
Al. hypsiphonus						+++	+++	++					
Al. obstetricans						+++	+++	++					
L. omissus						+++	+++	++					
L. crystallinoron							++						
L. zebra							N	++					

1. Records from western Nigeria refer either to *L. occidentalis* or to *L. boulengeri* (SCHIØTZ, 1967).
2. Records from blocks 7-9 (LAURENT, 1973) are doubtful.
3. Erroneously termed a bushland species by SCHIØTZ (1999) (AMIET, in litt.).
4. Doubtful records further east.

Source : MNHN, Paris

Table 1 (continued).

Species name	1	2	3	D	4	5	6	7	8	9	A	10	FN
H. mosaicus							N	N					
H. ghesquieri								++					
L. o. schiotzi									++				
L. c. meridionalis									+++				
A. equatorialis									+++	+++			
A. laevis						+++	+++	+++	++	+++			
H. ocellatus						+++	+++	+++	++	+++			
Ac. spinosus						+++	+++	++		+++			
L. millsoni						+++	+++	+++	++	+++			
L. c. calcaratus						+++	+++			+++			
L. o. ocellatus							+++			+++			
A. leucostictus									?	+++			
C. pictus										+			5
H. leleupi										+			5
H. frontalis										+			6
H. alticola										+			6
L. kivuensis										+			6
A. uluguruensis												+++	
L. parkeri												+++	
L. barbouri												+++	
L. vermiculatus												+++	
L. uluguruensis												+++	
H. tannerorum												N	
H. kihangensis												C	
TOTAL	11	8	1		3 (5)	19 (20)	20	11 (12)	6 (8)	13* (14)		7	

5. Montane, endemic to the Itombwe Plateau.
6. Montane, endemic to the Albertine rift mountains.
* Five species from the Albertine rift mountains omitted (see text).

Extrapolation of the distribution brings an element of subjectivity into this study. I believe this to be defensible especially in the many cases where vicariant taxa replace each other. But there is a danger that preconceived ideas about the zoogeographical units filter into published range maps, thus making appear legitimate what is in fact only a working hypothesis.

METHODS

Detailed taxonomic information on taxa are not provided here. Appendix 1 gives the complete list of taxa mentioned in the text, with their authors and dates and their taxonomic allocation (in families, genera, species and subspecies) according to FROST et al. (2006). Some recent information can be found in SCHIOTZ (1999), RÖDEL et al. (2003), AMIET (2000, 2001, 2004*b*, 2005), LÖTTERS & SCHMITZ (2004), DUBOIS et al. (2005), LÖTTERS et al. (2005) and KÖHLER et al. (2006).

Source : MNHN, Paris

Table 2. – Distribution of sylvicolous taxa, from Cross river to Angola, along transect Y-Z (fig. 2). In order to seek maximal resolution, in this table forest block 6 is subdivided after the lines shown on fig. 8. The area between lines F and G is block 5, that between G and K is block 6. FN, footnotes. For other abbreviations, see legend of tab. 1.

Species name	F	G	H	I	J	K	L	FN
Al. jynx	+							
Ar. krebsi	++							
A. schneideri	?							
H. acutirostris	+++	+						1
H. bopeleti	S	+						1
H. endjami	++	+++						1
H. mosaicus		+						2
A. laevis	+++	+++						3
L. zebra		(+)						4
L. crystallinoron			+					
Ch. koehleri	+++	++	++					
L. brevirostris	+++	+++	++					2
O. immaculatus	+++	+++		++				2
L. millsoni	+++	+++	++	++				3
L. calcaratus	+++	+++	++	++				3
L. rufus	+++	+++	++	++	++			1
Al. obstetricans	+++	+++	++	++	++			2
L. boulengeri	+++	+++	++		++			2
Al. hypsiphonus	+++	+++	++	++	++			2
L. omissus	+++	+++	++	++	++			2
Ac. spinosus	+++	+++		++	++			3
L. ocellatus		E	++	++	++			3
H. ocellatus	+++	+++	++	++	++			3
TOTAL	18 (19)	19	12*	10	8	0		

1. Confined to block 5 and (part of) block 6.
2. Also in south-eastern Cameroun, and presumably further east in block 7.
3. Also further east in the Congo Basin.
4. Distribution badly known. Found in south-eastern Cameroun, one record touches present area.

* BURGER et al. (in press) listed 30 treefrogs from south-western Gabon (sector I-J in present paper), including 7 or 9 unidentified species, but presented no information about habitat preference.

The forest-related treefrogs in tropical Africa are divided into sylvicolous and parasylvicolous species as further elaborated on pages 10-12 and in tables 1-4. A search for clusters in their distribution was undertaken. The result is that the parasylvicolous fauna does not fall into well-defined clusters, but the sylvicolous fauna does. Partly based on such clusters of sylvicolous species and partly based on recognized zoogeographical entities characterized by distribution of other animals (OLSON & DINERSTEIN, 1998), the forest was tentatively divided into ten forest blocks (p. 12). An attempt was made to characterize these forest blocks by their treefrog fauna and to assess the validity and significance of the blocks.

An attempt was made to make a hierarchical dendrogram illustrating the similarity between the sylvicolous treefrog faunas in the forest blocks using the Quotient of Similarity

Source : MNHN, Paris

(QS) (SØRENSEN, 1948): 2 × number of taxa common to both areas, divided by sum of totals of taxa from both areas × 100 (see p. 20 and fig 6).

The statement of close affinity between habitat and fauna is based on numerous observations of animals at the breeding site. Anecdotal evidence points at a less rigorous affinity outside the breeding season, where, however, observations are scarce.

The distribution data are taken from many sources, mostly compiled in SCHIØTZ (1999).

WHY TREEFROGS?

It has been shown earlier in a study from West Africa (SCHIØTZ, 1967) that the treefrogs seem well suited for a zoogeographical analysis, in fact better than other Amphibia. Especially the genus *Hyperolius*, which seems to be in a process of recent speciations, shows a finer geographical separation at the species- or subspecies-level through West Africa than most or all other genera. The genera *Afrixalus* and *Leptopelis* show less splitting-up, but still a significant one. Genera in other families are less suited for such an analysis, sometimes because their taxonomy is far less understood. For instance, the large genera *Phrynobatrachus* and *Arthroleptis* (only surpassed by *Hyperolius* in number of species), suffer from an unsettled taxonomy. To measure with confidence the level of taxonomic uncertainty is hardly possible, and is not always apparent from published fauna-lists, but an indication of the uncertainty is that J.-L. Amiet, a most meticulous worker in the best explored country in tropical Africa, Cameroun, only lists 3 certain names in the genus *Arthroleptis* out of a total of 12 species occurring in that country, and only 8 certain names out of 20 species of *Phrynobatrachus* (AMIET, pers. comm.). Such reservations, even from a very well-explored area, make the genera unsuited for continent-wise zoogeographical analyses. Amiet in comparison lists none of the 24 *Hyperolius* and none of the 16 *Leptopelis* taxa as taxonomically unsettled.

THE TWO FAUNAS IN THE AFRO-TROPICAL FOREST

As generally acknowledged, two well-defined faunas of Amphibia co-exist in the forest belt, sympatric but normally not syntopic. The first one is, at least in the breeding season and on breeding sites, strictly confined to reasonably undisturbed closed-canopy forests and has been termed the High Forest Fauna (SCHIØTZ, 1967, 1975, 1999). The other is confined to disturbed, often heavily disturbed forest, cultivated clearings in forests, dry forests and well-developed gallery forests in the humid savanna. The name Farmbush Fauna was used in SCHIØTZ, (1967, 1975) for this fauna, changed to the Bushland Fauna in SCHIØTZ (1999). The change, which may have been unfortunate, was undertaken because several colleagues, mainly those not familiar with the tropical moist lowland forests of Africa, had difficulties with the distinction between the two faunas and in understanding the name farmbush which

Source : MNHN, Paris

Table 3 Distribution of parasylvicolous taxa, from Sierra Leone to Angola, along transect W-Y-Z (fig. 2). Capital letters refer to "breaks" (see fig. 8) as distinct from the forest blocks of table 1. EW and EE delimit the Dahomey Gap. FN, footnotes. For other abbreviations, see legend of tab. 1.

Species name	A	B	C	D	Ew	Ee	F	G	H	I	J	K	L	FN
H. occidentalis	+++													
H. nimbae		E												1
K. cochranae		+++												
K. arboricola			+++	+++										
P. boulengeri W		+++	+++	W										2
H. picturatus		+++	+++	+++										
H. baumanni					+++									
H. f. fusciventris	+++	+++												3
H. f. lamtoensis			+++	?										3
H. f. burtoni				+++	+++		+++							3
H. f. ssp.								+++						3
L. hyloides	+++	+++	+++	+++	+++		+++							
H. c. concolor		+++	+++	+++	+++									
H. c. ibadanensis							+++							
H. c. ssp.								+++						
H. s. ivorensis			+++											
H. s. sylvaticus				+++										
H. s. nigeriensis							+++	+++						
H. guttulatus		+++	+++	+++			+++	+++	+++		++			
A. d. dorsalis		+++	+++	+++	+++		+++	+++	+++					
A. d. regularis										++	++	++	++	
P. boulengeri E							E	+++	+++					2
H. tuberculatus							E	+++	+++	++	++			
A. lacteus								+						4
H. r. riggenbachi								+						4
H. r. hieroglyphicus								+						4
H. camerunensis								C						5
L. notatus								+++	+++	++	++			
H. boettgebae								+++	+++					
H. kuligae								+++	+++					6
A. paradorsalis								+++	++	++	++			
H. dintelmanni									+					
H. pardalis									+++	+	++			
L. aubryi								++	+++	++	++	++		
H. phantasticus									+++		++	++		
H. platyceps									+++	++	++	++		
H. adspersus								+	++		++	++	++?	7
P. leonardi										++	++	++		
Cr. greshoffi										++	++	++		
H. cinnamomeoventris									+++	+	++	++	++	
A. osorioi													++	
TOTAL	3	9	9	9 (10)	5		8	17	15	10	13*	8	3 (4)	

1 Known only from a very small area near cutting line B
2 The widely separated *P. boulengeri* East and West are here treated as separate taxa
3 Possibly separate, vicariant species (RODEL & ERNST, 2003, RODEL et al., 2005)
4 Largely montane, endemic to the Cameronese ridge
5 Confined to a small area in Cameroun
6 Doubtful Uganda record
7 Distribution virtually unknown due to confusion with "*H. nasutus*"
* BURGER et al. (in press) listed 30 treefrogs from south-western Gabon (sector LJ in present paper), including 7 or 9 unidentified species, but presented no information about habitat preference

Source : MNHN, Paris

Table 4 Distribution of parasylvicolous taxa, from Cross river to the Indian ocean, along transect Y-X (fig. 2).

Only species ocurring east of Cross river are included. For species further west, see table 3. Numbers refer to forest blocks (fig. 4) since data are too incomplete to suggest dividing breaks. Block 6 is only touched in its northern part. Blocks 7, 8 and 9 do not form a linear sequence. For other abbreviations, see legend of tab. 1

Species name	5	6	7	8	9	A	10	FN
H. fusciventris	+++							1
H. concolor	+++							1
H. sylvaticus	+++							1
H. bopeleti	+++							
A. lacteus	+							2
H. r. riggenbachi	+							2
H. r. hieroglyphicus	+							2
H. cameruncnsis	+							
H. guttulatus	+++	++						3
A. dorsalis	+++	+++						3
P. boulengeri E	+++	N						
H. dintelmanni		+						
A. paradorsalis	+++	+++	W					
H. bolifambae	+++	+++	W					
L. aubryi	+++	+++	++					
H. adspersus	+	+++	W					4
H. kuligae	+++	+++	W					
H. pardalis		+++	++					
P. leonardi		S	W	W				
H. platyceps		+++	W	++				
L. notatus	+++	+++	+++	+++				
H. phantasticus		+++		+++				
C. greshoffi		+++	+++	+++				
H. tuberculatus	+++	+++	+++	+++	+++			
H. cinnamomeoventris		+++	+++	++	+++			
L. christyi			?		+++			5
A. osorioi			E	+++	+++			
K. mertensi				+	+++			
H. robustus				++	+			
P. verrucosus				+++	+++			
L. fizensis					++			
H. batsebanii					+			
H. castaneus					+			6
H. lateralis					+++			
L. mackayi					E?			7
H. kivuensis					+++			8
H. punctulatus							+++	
H. mitchelli							+++	
L. flavomaculatus							+++	
H. rubrovermiculatus							N	
A. sylvaticus							N	
P. keithae							+	9
TOTAL	18	17	13 (14)	11	13		6	

A so occurring further west (table 3)
2 Montane endemic to the Cameronese ridge
3 Occurring further west and south (table 3)
4 Distribution badly known
5 Cameronese populations may belong to a different taxon (AMIET 2004*a*)
6 Montane from Albertine rift mountains
7 Only known from western Kenya, possibly also in République Démocratique du Congo.
8 Also dense savanna south of forest belt
9 Habitat preference badly understood

Source : MNHN, Paris

is meaningless in the savanna and dry forests where farmed or degraded land harbour the same fauna as unfarmed land. To avoid such misunderstandings, I will instead use terms which may give fewer associations, namely *sylvicolous* for the High Forest Fauna, and *parasylvicolous* for the Farmbush/Bushland fauna, names proposed by AMIET (1989) – in French as *sylvicole* and *parasylvicole* – in addition to the term *savanicolous* for the savanna-living forms.

It was shown for West Africa (SCHIØTZ, 1967) and for Eastern Africa (SCHIØTZ, 1976, 1981) that the zoogeographical patterns for the sylvicolous and the parasylvicolous faunas differ profoundly from each other (and both differ profoundly from the pattern of the savanna fauna), so that the most "precise", and therefore most informative picture is obtained by keeping these faunas separate. This is therefore also done in this study.

The 103 forest-related treefrog species – 115 taxa when considering recognized subspecies – suited for analyses can be separated into 49 parasylvicolous and 54 sylvicolous species, or 59/56 when subspecies are considered, plus a few excluded species (app. 3). Since the separation into the geographically largely overlapping sylvicolous and parasylvicolous faunas can only be undertaken based on a thorough field-knowledge of the forms, there is a certain element of subjectivity in this separation and it can hardly be expected that workers in different parts of the forest belt agree completely on the distinction between sylvicolous and parasylvicolous species. It might, however, be relevant to compare this distinction in two comparable areas covered by different workers, namely the rather well-investigated West Africa west of the Dahomey Gap (mainly Schiøtz and Rödel, compilation in SCHIØTZ, 1999 and RÖDEL, 2000) and the very well investigated Cameroun (mainly Mertens, Perret and Amiet, compilation in PERRET, 1966 and AMIET, pers. comm.). West Africa has 14 species of sylvicolous treefrogs, 13 parasylvicolous; Cameroun has 22 and 23 respectively. These ratios could indicate that the distinction between the two faunas by the two set of workers is congruent, supported by the fact that Amiet's and my references to habitat type for the species we both know from the field is identical.

Practical field experience is deemed necessary. The division in this paper is thus based on the author having encountered 81 of the 115 treated taxa in the field, supplemented with Amiet's field experience of an impressive 46 taxa out of a total of 48 in Cameroun, of which 21 have not been encountered in the field by me (AMIET, 1986 and in litt.). Habitat preference for the taxa encountered neither by Amiet nor by me is given by a number of other authors, accepted here since there is no disagreement with these authors' general allocation of species to habitat. A compilation of data for distribution and habitat preference is found in SCHIØTZ (1999), supplemented with data found in the description of more recently described species (see DUBOIS et al., 2005). Only a recent paper by WIECZOREK et al. (2000) differs profoundly from the present paper in its allocation of *Hyperolius* to habitat (discussed further p. 30). In spite of his many years in Africa, Laurent, the authority on the African treefrogs, only rarely mentioned habitat affinity in his papers.

It should be noted that the habitat affinity, even of the rarer taxa of which only few specimens have been collected, is normally based on many records of voices where the collectors especially would investigate frogs calling from an unusual place. Exceptions from the habitat affinity should therefore be stressed rather than downplayed by our collecting methods. Since it is to be expected that every species has its own ecological requirements and

Source : MNHN, Paris

preferences it is not surprising that some species do fall outside this rigorous division, sometimes perhaps because of a broader requirement, sometimes perhaps by requirements not expressed by the sylvicolous/parasylvicolous division. Such species are dealt with in appendix 3.

Amiet has in his later papers (first AMIET, 2001) introduced the term *phonocénose* for the "sound-scape" in which the calling males are found, "des ensembles d'espèces qui exercent leur activité vocale... pendant la même période de l'année et dans des sites présentant des caracteristiques écologiques similaires". He uses this concept in addition to, not replacing, his distinction between sylvicolous and parasylvicolous species. This term is perhaps a more precise definition of what I have called "faunas", for strictly speaking we know very little of the affinity to the vegetation outside the breeding season and breeding sites. Very few specimens are collected outside the breeding season and breeding sites, and there is some anecdotal evidence that some migration through "alien" vegetation occurs, at least for savanicolous and parasylvicolous species (SCHIOTZ & DAELE, 2003: 143; AMIET, in litt.). On the other hand, the term phonocénose may be too narrow for the present purpose since, at least within the sylvicolous species, some are connected with small streams, others with small stagnant swamps, etc. They may not belong to the same phonocénose, but are here regarded as belonging to the same fauna. Also the timing of breeding activity in the rainy season may separate species belonging to the same fauna into different phonocénoses.

Poynton, in several papers, expressed some reservation as to the link between Amphibia distribution and vegetation (e.g., POYNTON, 1962: 34: "large-scale faunal patterning which is determined mainly by the vegetation patterning should be treated with a great deal of caution"). My approach, however, is to regard affinity to the vegetation types as the fundamental basis for the distribution of the species. We do not know specifically which factors are decisive, but field observation (not only of frogs) demonstrates clearly this dependence, and it is extremely rare to find specimens in "the wrong vegetation". Microclimate, so dramatically different especially between savanna and closed canopy forest, may be one factor. This could explain POYNTON's (2000*b*) observation that species which are forest-limited in lowlands, sometimes occur in open formations at high altitude.

The smallest recognised systematical unit, subspecies, is used in this paper. It is noteworthy that no cases are known of different subspecies within a species occupying different habitats. Habitat affinity seems to be a fundamental species character. The two faunas, sylvicolous and parasylvicolous, are thus taxonomically separate at species level, and are approximately of similar magnitude of species diversity in any given area.

FOREST BLOCKS

A basis for the present study is the forest ecoregions proposed by the World Wildlife Fund (WWF) in their "Global 200" study (OLSON & DINERSTEIN, 1998). WWF's division into ecoregions is a consensus result of wide consultations with workers familiar with different animal and plant groups. An ecoregion is defined by WWF as "a geographically distinct assemblage of natural communities that share a large majority of their species, ecological dynamics and environmental conditions". This division differs somewhat from that proposed

Source : MNHN, Paris

by POYNTON (1999), whose definition of regions is more pragmatic "a region is... an area covered by a perceived set of species ranges". Another definition – even more pragmatic is that of NOBLE (1924, 152) for his biogeographical regions: "convenient areas for distributional discussion".

Since several of WWFs ecoregions invite to further subdivision when looking at the fauna of treefrogs, several of them has been subdivided in this paper into forest blocks based on a perceived set of species ranges. In this paper, the term forest block is used for all the units studied here. Unfortunately, the terminology for blocks used here is not directly comparable with the divisions in POYNTON (1999) (app. 2).

THE SYLVICOLOUS FAUNA

DISTRIBUTION

In this study, ten forest blocks (fig. 1) are tentatively recognised as a basis for discussion of the distribution of the sylvicolous fauna. They are a result of my analyses of the distribution of the sylvicolous fauna. The parasylvicolous fauna has not contributed to their characterization. The validity and significance of these blocks are described and discussed in this and the following chapter and tables 1-2.

Block 1. Liberia Block

Distribution. – From western Guinea, western Senegal and Sierra Leone to V baole which is a tongue of savanna stretching almost to the coast along Bandama river in eastern Côte d'Ivoire.

Knowledge. – Well explored (LAURENT, 1958, GUIBÉ & LAMOTTE, 1958; RÖDEL, 2000, SCHIØTZ, 1967).

Description. – Forest degraded and fragmented. The westernmost part (western half of Sierra Leone, western Guinea and Senegal) seems to harbour a dry part of the forest with only one sylvicolous species, *Hyperolius chlorosteus*, recorded. The parasylvicolous fauna it this part is distinctive (p. 26).

Endemics. – *Hyperolius chlorosteus*; **H. menokouensis*, *H. wermuthi*, *H. zonatus*, **Kassina lamotte*. Species marked with * are only recorded from the central part of the region.

Block 2. Gold Coast Bloc

Distribution. – Eastern part of Côte d'Ivoire from V-baole eastwards to Volta river in eastern Ghana.

Knowledge. – Rather well explored (SCHIØTZ, 1967).

Source : MNHN, Paris

Description. – Forest much degraded and fragmented.

Endemics. – *Hyperolius bobirensis*; *H. laurenti*; *H. viridigulosus*. The latter occurs also in the easternmost part of block 1, east of river Sassandra.

Block 3. Trans Volta-Togo

Distribution. – A narrow peninsula of forest-clad hills and low mountains in Ghana east of Volta river and in western Togo.

Knowledge. – Not well explored (SCHIØTZ, 1967, RÖDEL & AGYEI, 2003).

Endemics. – Two endemic treefrogs, the parasylvicolous *Hyperolius baumanni* and the sylvicolous *H. torrentis*.

Block 4. Southern Nigeria

Distribution. – From the Dahomey Gap (or Benin Gap) to Cross river.

Knowledge. – The parasylvicolous fauna is well explored, the sylvicolous fauna that may exist in the few and scattered remaining forests is almost unexplored (SCHIØTZ, 1967).

Description. – Southern Nigeria from the border with Benin to Cross river is today a forest-savanna mosaic so heavily influenced by man that closed-canopy forests are few and scattered. These forests have not been the subject of qualified collection, so the sylvicolous fauna, if still existing, is almost unknown. Collections indicate one, possibly two sylvicolous species belonging to western blocks (*Afrixalus nigeriensis*; possibly *Leptopelis occidentalis*), a few to the eastern (*Ophistothylax immaculatus*; *Leptopelis brevirostris*, possibly *L. boulengeri*).

Block 5. Cross-Sanaga Coastal Forests

Distribution. – From Cross river in eastern Nigeria to Sanaga river in Cameroun, covering the coastal lowlands and the forested parts of the Cameronese ridge.

Knowledge. – Very well explored (PERRET, 1966; AMIET, 1986). Unpublished fauna list distributed privately by Amiet in 2004 (AMIET, pers. comm.).

Description. – The lowlands are today a mosaic of humid forest, degraded forest and farmland. Mount Cameroun and the Cameronese ridge have a number of species often regarded as montane but, according to Amiet (in litt.), only *Afrixalus lacteus* is strictly so.

Endemics. – "Montane" species, endemic to the ridge, are: *Hyperolius riggenbachi* (found also at low altitude on the Benue plains), *Afrixalus lacteus* and some populations of *Leptopelis modestus*. In lowlands, *Arlequinus krebsi*, *Alexteroon jynx* and the enigmatic *Afrixalus schneiderei*.

Block 6. Congolian Coastal Forests

Distribution. – Stretching from Sanaga river in Cameroun in a belt along the Atlantic coast to Angola. South of Cameroun, the vegetation is a mosaic of forests and savannas. The eastern

Source : MNHN, Paris

limit towards block 7 is not well defined. The southern limit seems to coincide with the border Angola-République Démocratique du Congo although one, probably two parasylvicolous species, *Afrixalus dorsalis* and probably *Hyperolius adspersus*, are found as far south as coastal central Angola

Knowledge. Northern part (Cameroun) is very well explored (see under block 5) Scattered collections from further south: mount Alen, Equatorial Guinea (LASSO et al., 2002; RIVA, 1994), central Gabon (FRETEY et al., 1998, 2001), south-western Gabon (BURGER et al., 2004), south-western République du Congo (LARGEN & DOWSETT-LEMAIRE, 1991) and Mayombe, coastal République Démocratique du Congo (LAURENT, 1943, 1972, 1976, 1982).

Description. The northern, well explored part (Cameroun) has one endemic species, *Hyperolius dintelmanni*, and shares the following with block 5: *H. acutirostris*, *H. bopeleti* and *Chlorolius koehleri* *Hyperolius endjami* and *Leptopelis rufus* are endemic for block 5 and 6. In north-western Gabon, *Leptopelis crystallinoron* is found Several species are common for block 5 and 6 and furthermore occurring to the east (table 2) Otherwise this region is characterised by the occurrence of a number of West African parasylvicolous species (p. 26) No sylvicolous species is known south of the border Angola-République Democratique du Congo.

Block 7. North-western Congolian Forests

Distribution. – Preliminary delimitation are Ubangi and Congo rivers and to the west the Congolian Coastal Forests.

Knowledge. – The part of the forested Congo cuvette situated in south-eastern Cameroun has been explored by Amiet but, according to him (in litt.), needs further research. The remaining area is virtually unexplored. The entire Congo basin (blocks 7, 8, 9, part of 6) has been covered by papers by LAURENT: *Hyperolius* (1943), *Leptopelis* (1972*b*), *Cryptothylax*, *Kassina* and *Phlyctimantis* (1976), *Afrixalus* (1982). Outside of the three old national parks these papers, however, are based on scattered and limited material. Of these parks only part of one, Parc National des Virunga, is within the scope of the present paper.

Endemics. – No endemic treefrogs are known for this block.

Note. The Congo-Lualaba and Ubangi rivers are regarded by WWF (OLSON & DINERSTEIN 1998) as borders between ecoregions – here listed as 7, 8 and 9. It may seem doubtful if rivers in the wettest forest or swamp forest along them really are major zoogeographical borders for Amphibia.

Block 8. Central Congolian Forests

Distribution. The forested parts of the Congo basin, south of the Congo-Lualaba river.

Knowledge. The least known of the ecoregions. Only few, scattered collections (SCHIØTZ, 2006)

Source : MNHN, Paris

Endemics. *Cryptothylax minutus*, *Kassina mertensi*, *Hyperolius ghesquieri*, *H. robustus* and *H. sankuruensis* are recorded only from this region, but since they all are known only from a single or very few localities, their real distribution is unknown.

Block 9. North-eastern Congolian Forests

Distribution. East of Ubangi river, north and east of Congo-Lualaba river, here taken also to include forests at medium altitude in Uganda and westernmost Kenya. In WWF's Global 200 (OLSON & DINERSTEIN, 1998), the eastern border is set at the Albertine rift.

Knowledge. Virunga National Parc (mainly savanna-forest mosaic) is well explored (LAURENT, 1950, 1972*a*), but in spite of large collections the sylvicolous lowland fauna is virtually unknown. There are lowland collections mainly from the Ituri area (NOBLE, 1924, names updated by POYNTON, 1998) and from montane western Uganda (DREWES & VINDUM, 1994), and collections from forests at low and medium altitude in Uganda and western Kenya (SCHIØTZ, 1975; SCHICK et al., 2005). Otherwise very few collections exist. The suggested border areas between this block and blocks 7 and 8 are quite unexplored.

Endemics. From lowland, the imperfectly known *Hyperolius ferrugineus* and *H. langi* (appendix 3). *Afrixalus leucostictus* may also be endemic: one doubtful record exists from block 8 (LAURENT, 1982), this specimen has been examined, and I find it impossible to decide whether it is *A. equatorialis* or *A. leucostictus*. Endemic are also the parasylvicolous *Leptopelis fiziensis*, *L. mackayi*, *Hyperolius lateralis* and *H. hutsebauti*.

The Albertine Rift mountains and highlands harbour a number of montane forest-related treefrogs, all endemic to these mountains, several of them very poorly known and with no ecological information: *Callixalus pictus*, *Hyperolius frontalis*, *H. alticola*, *H. castaneus*, **H. chrysogaster*, **H. diaphanus*, *H. leleupi*, **H. leucotaenius*, **H. xenorhinus*, **Leptopelis fenestratus* and *L. kivuensis*. Those with an * are omitted in this study because of lack of information about habitat.

Block 10. Eastern Forests

Distribution. The forest block, as here understood, consists of small patches of moist, closed-canopy forests in eastern Tanzania and Malawi (Eastern Arc mountains and outlying mountain blocks to the south) with a mixture of sylvicolous and parasylvicolous species, and of areas of dry, semi-deciduous forests in the lowland to the east and south-east of the Eastern Arc with a mixture of parasylvicolous and savanicolous species. The dry forests form a mosaic with Miombo Woodland from coastal Kenya to north-eastern South Africa. This latter area has been termed eastern lowlands (SCHIOTZ, 1976; POYNTON, 1995, 1999). The southern border of this block is here set at approximately 22°S, which seems to represent the southern limit of the parasylvicolous tropical fauna of treefrogs (*Leptopelis flavomaculatus*, *Hyperolius punctulatus* and *H. mitchelli*). Other parasylvicolous species occurring further south, in South Africa, are not treated in this study.

The eastern forests are separated from the forests in Central and West Africa by an impressive gap of dry savanna, approximately 500 km wide or more, termed "the arid corridor" by POYNTON (1995).

Source : MNHN, Paris

Knowledge. – Well explored (SCHIØTZ, 1975, POYNTON, 2000*b*).

Endemics. The entire sylvicolous and parasylvicolous fauna in this block is endemic.

Description. It is important to note that the large forest block "Eastern Forests" as here understood differs profoundly from the other forest blocks: whereas these other blocks have closed canopy forest ("rainforest") as their climax vegetation and have been almost totally forest clad until the influence of man, the climax vegetation in the eastern forests outside of the Eastern Arc is either dry, semi-deciduous forest or forest-savanna mosaic. Only on the Eastern Arc and a few areas to the south of them is the climax vegetation moist evergreen forest with a sylvicolous fauna. The distinction between forest types versus the distinction between a montane and a lowland fauna is discussed on p. 19.

DISCUSSION

Tables 1 and 2 summarize the distribution along transect lines (fig. 2), subdivided in table 2 as in fig. 8.

The sylvicolous fauna shows a complete separation at species level between the three major regions with the Dahomey Gap or southern Nigeria as one divide, the Arid Corridor as the other. These regions are thus: (1) West Africa west of the Dahomey Gap; (2) Central Africa from southern Nigeria eastwards, (3) the forests of the Eastern Arc mountains. These regions can be subdivided into a number of forest blocks as indicated above (fig. 1).

The West African forest blocks 1 to 3 are reasonably well explored, well defined and well delimited. They differ most conspicuously in the genus *Hyperolius* for which each block has its distinct fauna of sylvicolous species. Three of the endemic species in block 1 are only known from the central part of the block, western Côte d'Ivoire (*Kassina lamottei*, *Hyperolius uenmuthi* and *H. menokouensis*). This central part of the block is the best investigated, which might explain why these secretive species were found there, or the species may be confined to the wettest, central part of the block, as suggested by RÖDEL (in litt.).

The blocks west of the Dahomey Gap (blocks 1-3) are completely separate at species level from block 5 and eastwards, but the badly explored – and much degraded – southern Nigeria (block 4) seems to represent a transition, with the occurrence of the western *Afrixalus nigeriensis* and the eastern *Opisthothylax immaculatus* and *L. brevirostris*. Either the western *L. occidentalis* or the eastern *L. boulengeri* were collected there (SCHIØTZ, 1967).

Blocks 5 and 6 have today a confluent forest cover, but with signs (patches of savanna) of having formerly been divided by a savanna tongue along the Sanaga river (AMIET, 1987). In a study of some typical Cameronese amphibia – not including any treefrogs –, AMIET (1987) has demonstrated the importance of the Sanaga river as a border between several species or subspecies pairs, such as *Leptodactylodon a. albiventris* versus *L. a. bueanus*, *Leptodactylodon ovatus* vs. *L. ventrimarmoratus*, *Astylosternus diadematus* vs. *A. batesi*, and *Cardioglossa nigromaculata* vs. *C. gratiosa*. In general the difference in the treefrog fauna in Cameroun north and south of the Sanaga river is not conspicuous (AMIET, in litt.). *Arthroleptis krebsi* and *Alexteroon proni* are endemic to the northern block, *Hyperolius mosaicus* occurs only south of

Source : MNHN, Paris

the river whereas *Hyperolius acutirostris* and *H. endjami* are common to block 5 and the northern, Cameronese part of block 6 *Leptopelis rufus* seems endemic to the entire blocks 5 and 6

The fauna of block 6 is not very distinct. Almost all the sylvicolous treefrogs known from this block are found also in block 5 to the north and/or in blocks 7-8 further east (table 2) The part of block 6 situated south of the Cameronese border seems poorer in species (both sylvicolous and parasylvicolous) than the Cameronese part of block 6 It cannot be said whether this is due to the fauna becoming poorer south of Cameroun as is the case when moving from Cameroun to the west or because there has been far less collecting effort in this area.

Block 7, south-eastern Cameroun and north-western Congo, has no sylvicolous species distinct from block 6. This is probably not due to lack of collecting, for although much of region 7 is virtually unexplored, its north-western corner (south-eastern Cameroun) is well explored. Of block 7, only the north-western corner, in Cameroun, is explored, of block 9 only the north eastern, leaving a virtually unexplored gap of more than 1000 km, and we completely lack collections showing whether the suggested borders between the blocks or ecoregions in WWF's terms 7, 8 and 9 (Congo and Ubangi rivers) are well-defined faunal breaks, or whether the fauna changes gradually

Block 8 is the least explored of the recognized blocks, since only scattered, rather unsystematic collections have been made Attempt by the author to collect in this block in 1975 and 2005 met only with limited success and could confirm an impression of a species-poor fauna. The five apparent endemic species for this region are so badly known that nothing can be said of their real distribution.

Block 9 has apparently only one endemic sylvicolous lowland species (*Afrixalus leucostictus* albeit with one doubtful locality in block 8), in addition to a number of species confined to highlands at the Albertine rift. In the lowlands outside these mountains the numbers of sylvicolous species are low (5) which seems difficult to explain except as a collection artefact, remarkable in view of the large collections made in Parc National des Virunga, also in its low-lying, partly forested parts (LAURENT, 1950, 1972) Large collections by non-specialists do, however, not necessarily mean that all species are ultimately found. Only 3 sylvicolous *Leptopelis* and no sylvicolous lowland *Hyperolius* reported from this area would point towards grave under-collecting.

Forest block 10, Eastern Forests, has a fauna, both sylvicolous and parasylvicolous, completely separate at species level from the fauna of the remaining blocks. The sylvicolous fauna is almost exclusively found in the forests of the Eastern Arc where local topography has ensured sufficient rainfall to maintain a closed canopy forest also through drier periods. Considering the minute size of these forests, probably also in the past, the fauna is quite rich. The forests are today split into a number of isolated units the best explored of which are eastern Usambara, western Usambara, Uluguru and Udzungwa. The distribution pattern between these isolated forest "islands" seems very similar to the pattern of the two major West African regions, 1 and 2, namely that the genera *Leptopelis* and *Afrixalus* have species in common for these "islands", whereas the two known sylvicolous *Hyperolius* seem endemic to one of the islands. The distributions of these sylvicolous *Hyperolius* are, however, not well known – both species are only known from the type locality – and they may be more widely

Source : MNHN, Paris

distributed, so no attempt was made to divide the Eastern Arc Forests into separate forest blocks on this slender evidence. The dry forests in the lowlands, including the coastal forests, harbour a parasylvicolous fauna (p. 26).

The fauna and flora in the Eastern Arc Forests is conventionally termed a montane fauna and flora (e.g., LOVETT, 1988, 1990; POYNTON, 1990, 1999, 2000, POYNTON et al., 2006) as different from the lowland fauna, the forest-related fauna in the eastern lowlands. I have in the present study preferred to distinguish between a sylvicolous and a parasylvicolous fauna rather than between a montane versus lowland fauna. Although we do not know the causal connections between altitude and/or vegetation and the distribution of animals, I do find such a distinction more relevant for a study of the treefrogs since the known altitudinal ranges (app. 4) do not seem to support a distinction based on altitude. The sylvicolous fauna is found as far down as the closed canopy forest (to 200 m on eastern slopes of the Usambaras), whereas the parasylvicolous fauna is found as far up as the right habitat (degraded forest and farmland) is found in the Eastern Arc mountains as well as in dry forest in the lowland. The closed canopy forest seems to harbour the sylvicolous fauna of treefrogs regardless of its altitude, and the degraded forests harbour the parasylvicolous fauna regardless of its altitude. Some species (*Hyperolius tannerorum*, *H. kihangensis* and *Phlyctimantis keithae*) were only recorded from localities higher than 1400 m, but since they are only known from one or a few localities it is unclear whether they are confined to such altitude. I do not see a dramatic deviation from common thinking by viewing the distribution of the treefrogs from a sylvicolous/parasylvicolous perspective rather that one determined by altitude, remembering Hengeveld's dictum, cited in POYNTON & BROADLEY (1991): "[biogeographical] classifications are not right or wrong, only useful or not".

The general picture for the sylvicolous treefrogs in tropical Africa is that the genus *Hyperolius* shows the maximal species diversification (fig. 3) with distinct species in each forest block. This is clearly the case in Western Africa and along the Atlantic Coast (blocks 1-5 and the northern part of 6), whereas the data for Central Africa (blocks 7-9) are far too incomplete to draw any conclusion. In fact, the only sylvicolous *Hyperolius* we know from these regions are known from single localities. In the well-explored Eastern Forests, the only known sylvicolous *Hyperolius*, *H. tannerorum* and *H. kihangensis*, seem to be confined to one forest each (western Usambaras and Udzungwas), although they may have been overlooked elsewhere.

Hyperolius ocellatus seems to be the only sylvicolous *Hyperolius* breaking this pattern, being found in blocks 5, 6, 7, 8 and 9. It may be significant that this is a species being both sylvicolous and parasylvicolous (AMIET, 1986, in litt.), although predominantly sylvicolous.

The genera *Leptopelis* and *Afrixalus* are more widely distributed (fig. 4), in most cases so that one set of species is found in West Africa (block 1-3), another in Central Africa (5-9) and yet another in the Eastern Forests. *Alexteroon* may belong to this group, although the distribution of its three members outside of Cameroun is badly known.

Finally, there is a group of sylvicolous amphibia with a wide distribution in blocks 1 to 9, namely, with our present understanding of their taxonomy, some *Bufo* and *Ptychadena*, and the only sylvicolous rhacophorid, *Chiromantis rufescens*. No sylvicolous Hyperoliidae or *Leptopelis* has such a wide distribution (fig. 5).

Source : MNHN, Paris

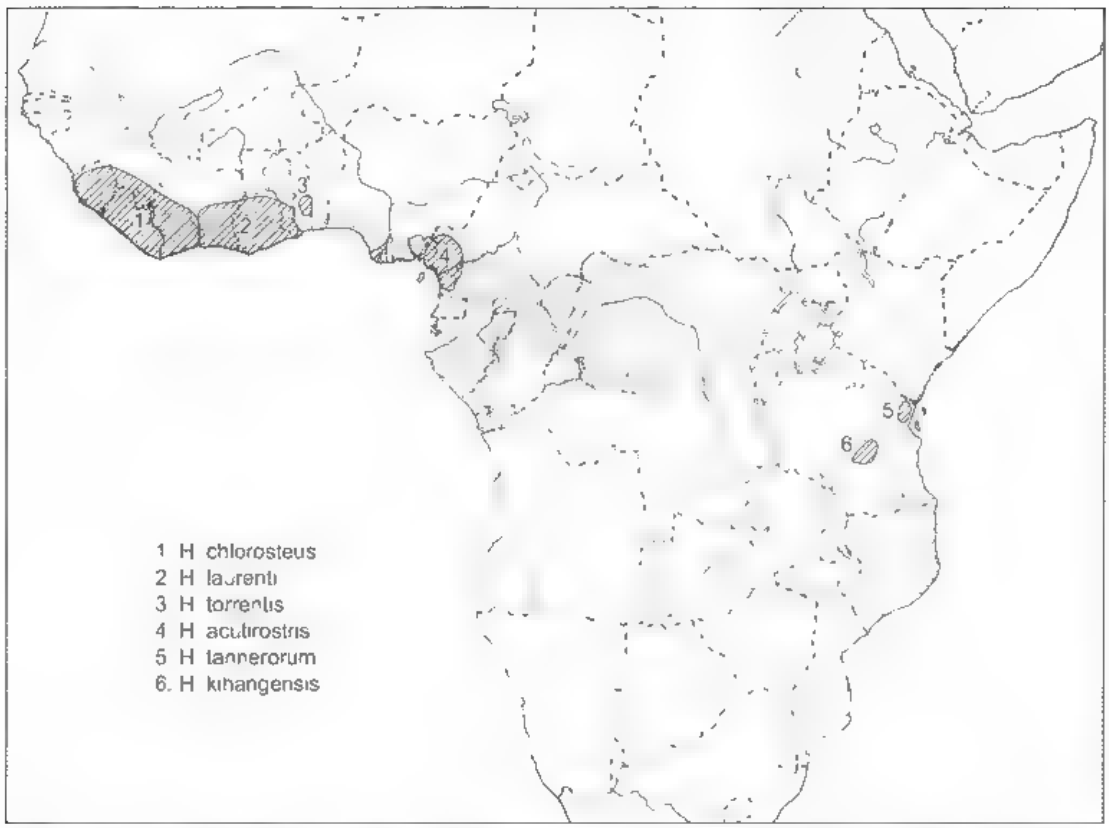


Fig 3 Maximal species diversification in sylvicolous Amphibia This pattern is shown by sylvicolous *Hyperolius* Our knowledge of the sylvicolous *Hyperolius* in the Congo basin is not sufficient to indicate distribution here

The genus *Kassina* has only one sylvicolous member, *K lamotte* from western Côte d'Ivoire, *Phlyctimantis* and *Cryptothylax* none The genus *Acanthixalus* is so cumbersome to collect that little can be said about its real distribution One species is known from two localities in West Africa, the other species from a few widely scattered localities in Central Africa. *Opisthothylax* consists of one sylvicolous species in Central Africa.

An attempt is made to make a hierarchical dendrogram illustrating the similarity between the sylvicolous treefrog faunas in the forest blocks (fig 6) through the Quotient of Similarity (QS) (p. 7) The QS should in the present case be taken with great reservation since several blocks are badly explored and/or the number of taxa is so low that the discovery of a single or a few taxa may change its value considerably Therefore blocks 3 and 4 have been omitted and 7, 8 and 9 combined Block 10 has been divided into three units, Usambaras (10a), Ulagurus (10b) and Udzungwas (10c) The difference between these reflects the occurrence of the two sylvicolous *Hyperolius*, which may or may not be endemic to Usambaras and Udzungwas respectively An attempt is also made to show similarity between block 5 and those parts of blocks 6 and 7 situated within the well-explored Cameroun in order to analyse similarities between areas with comparable exploration.

Source : MNHN, Paris

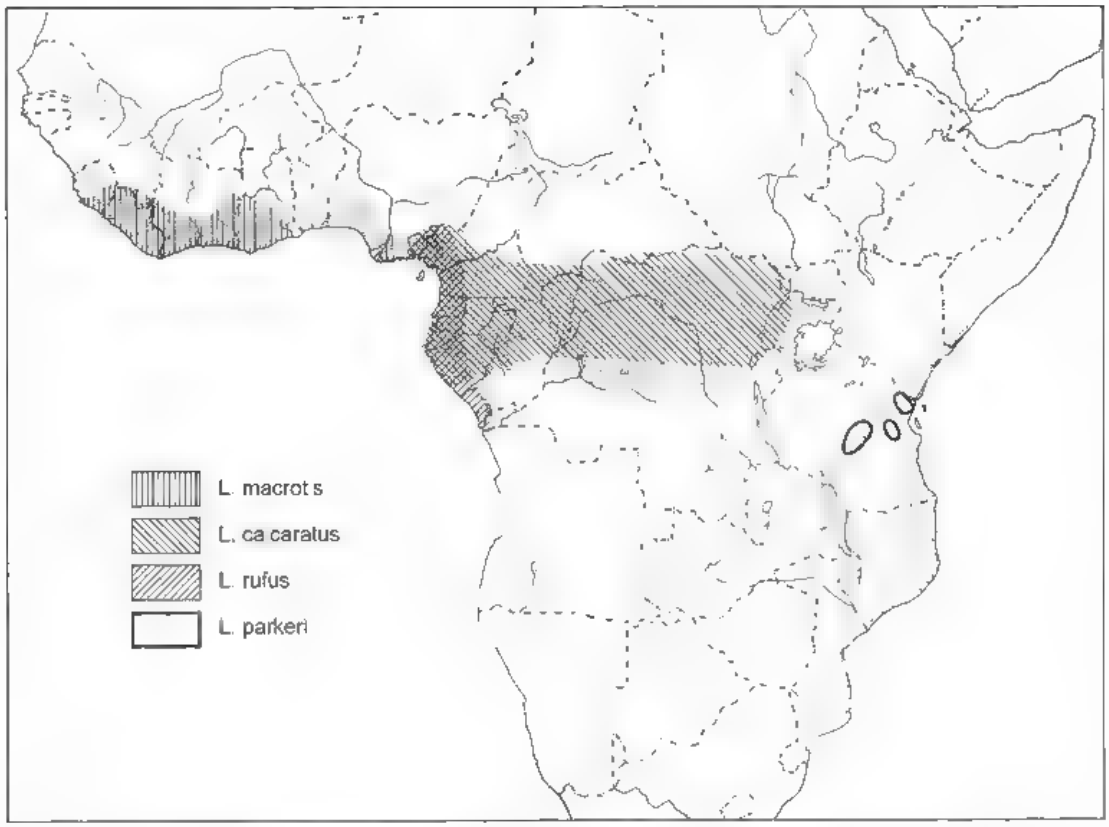


Fig 4 Medium species diversification in sylvicolous Amphibia This pattern is shown by sylvicolous *Leptopelis* and *Afrixalus*

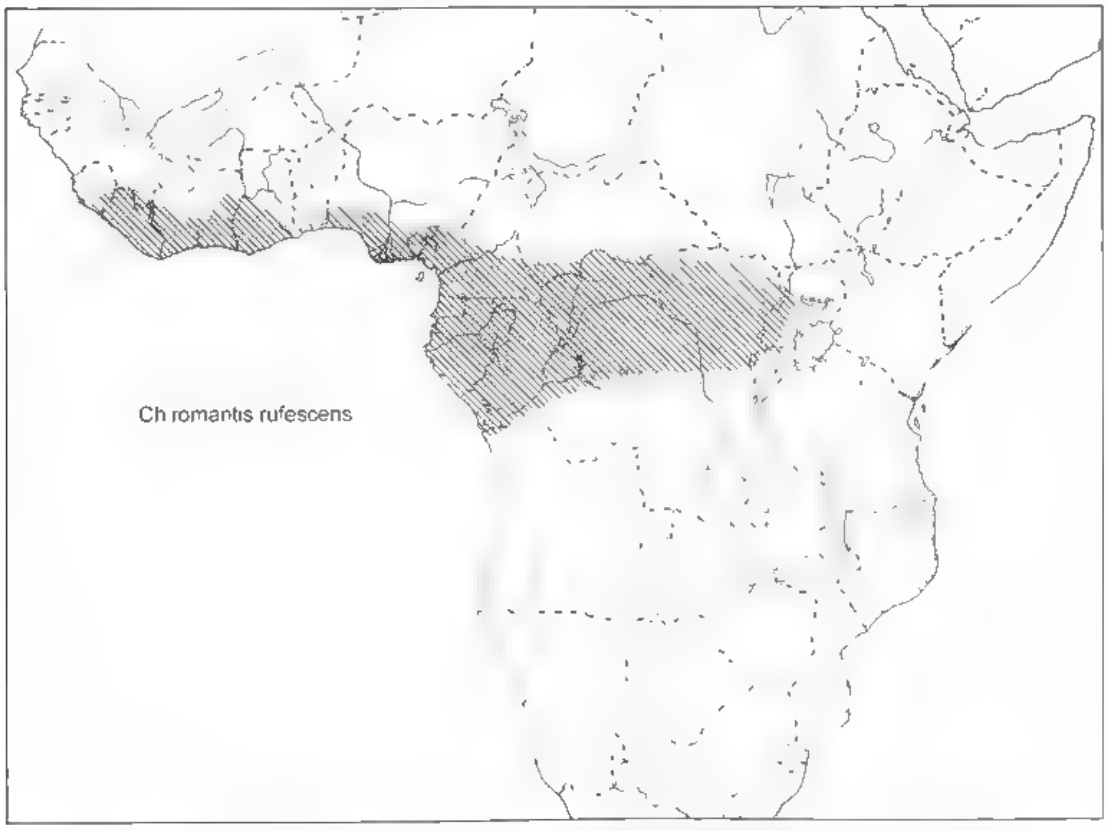
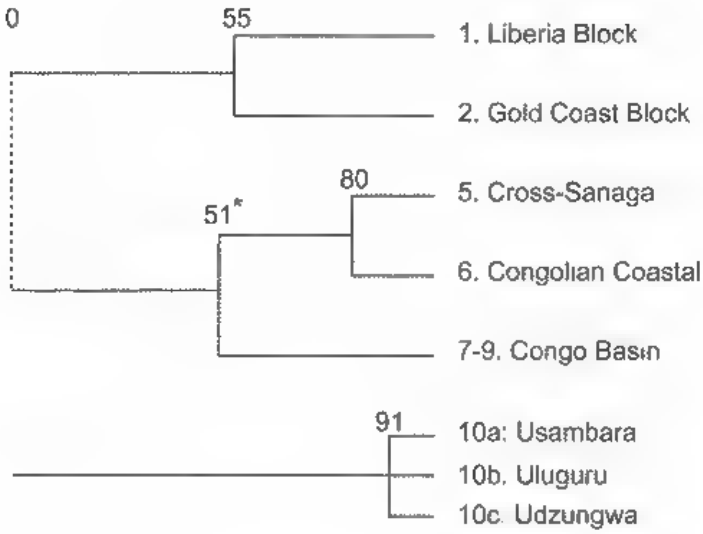


Fig 5 Minimal species diversification in forest Amphibia This pattern is not shown by any Hyperolidae or *Leptopelis*

Source - MNHN, Paris



	5	6n	7nw
5	-	82	64
6n		-	53

	10a	10b	10c
10a	-	91	83
10b		-	91

Fig 6 Quotient of Similarity between sylvicolous Amphibia in forest blocks. See text for explanation *, QS between 5+6 versus 7-9.

The two tables show in greater details the QS between selected areas.

There are no common taxa between the three "ecoregions", blocks 1-2, 5-9 and 10 When a possible connection between 1-2 and 5-9 nevertheless is indicated in fig 6, is it because it could be argued that these regions show similarity in their faunas through species pairs, probably closely related The West African *Leptopelis macrotis*, *L. occidentalis*, *Afrixalus vibekensis* and *Acanthixalus sonjae* may thus have "sister species" in Central Africa, namely *L. rufus* or *L. nullsoni*, *L. boulengeri*, *Afrixalus laevis* and *Acanthixalus spinosus*. An additional argument is also that several members of other families, such as *Chiromantis rufescens*, several *Bufo*, etc , are in common between these ecoregions. Block 10 has only one species, *Afrixalus uluguruensis* showing similarity to a Central African form, *A laevis*. The four *Leptopelis* seem dissimilar to any of their Central African counterparts. It can therefore be argued that the sylvicolous fauna of West and Central Africa may have a common root, whereas the fauna of the Eastern Arc Forests has developed independently of the rest of Africa's forest treefrogs.

Source : MNHN, Paris

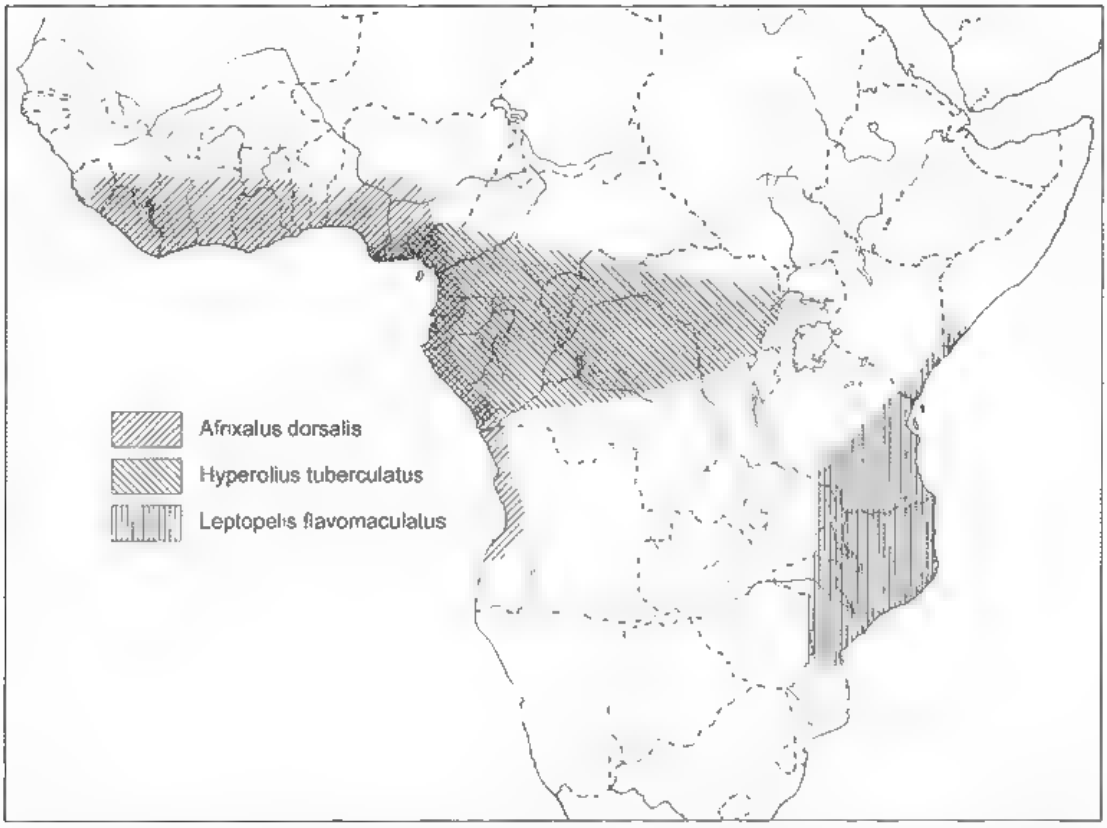


Fig. 7 The three typical distribution patterns found among the parasylvicolous treefrogs: a West African distribution (*Afrixalus dorsalis*, the species which is found further to the South), a Central African distribution (*Hyperolius tuberculatus*) and an East African distribution (*Leptopelis flavomaculatus*)

THE PARASYLVICOLOUS FAUNA

DISTRIBUTION

The distribution of the parasylvicolous fauna shows a pattern fundamentally different from that of the sylvicolous fauna. The overall picture is of three separate regions where, however, the borders between two of them differ from those of the sylvicolous faunas (fig. 7):

(1) A western fauna found throughout West Africa and further south in a belt along the Atlantic coast of Central Africa (blocks 5 and 6). *Afrixalus dorsalis* and probably *Hyperolius adspersus* are found as far south as coastal central Angola, the other species taper out farther north along the coast (table 3 and fig. 8). It is noteworthy that none of these West African species are found further inland in Central Africa into block 7, in spite of lack of obvious physical or vegetation barriers.

Source : MNHN, Paris

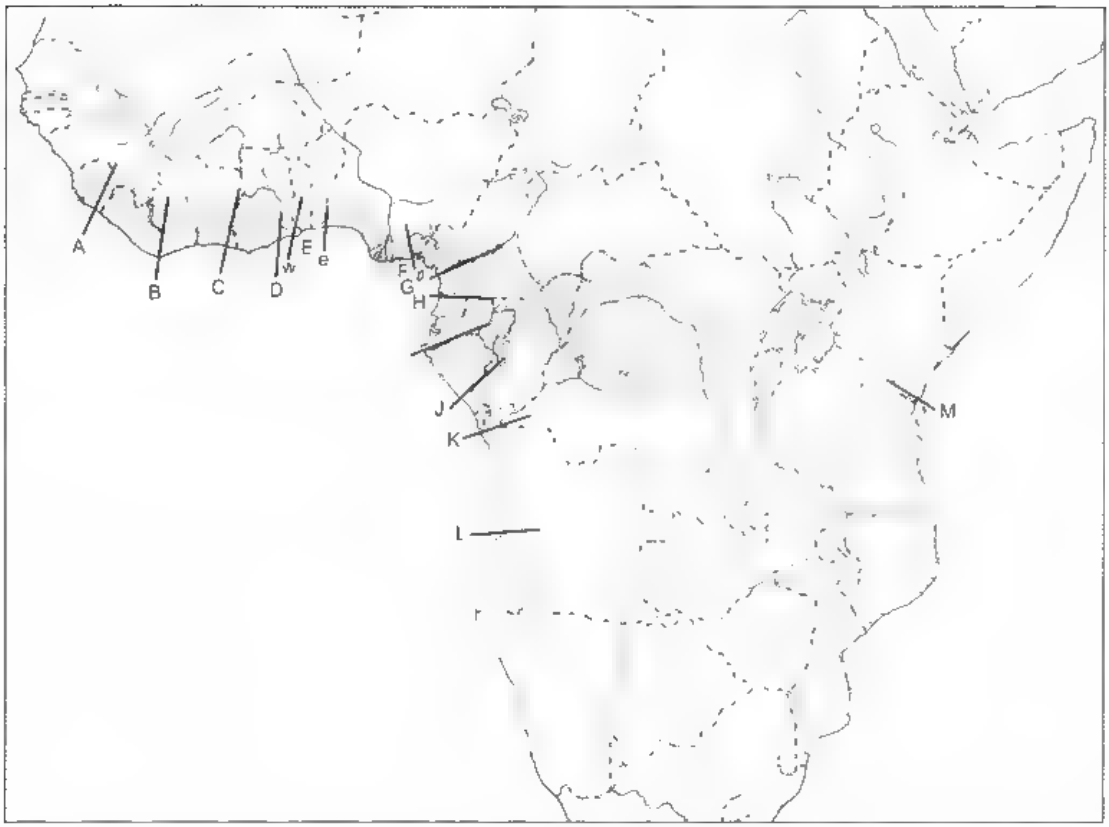


Fig 8. – Boundaries in the distribution of parasylvicolous treefrogs.

The lines A-G are based on a dense network of collecting localities and in most cases on the occurrence of vicariant taxa on either side of the line. In contrast, the credibility of the boundaries H-K is basically different since collecting there was so sporadic that arbitrary lines had to be drawn based on the scattered collections, and placed roughly between such collecting localities and between the refuges proposed in fig. 9. Available data do not permit to conclude that the boundaries between several pairs of vicariant taxa coincide exactly, even when this map implies so.

A, Eastern limit for *Hyperolius occidentalis*, and western limit for *H. picturatus*, *H. concolor* and *Afrixalus d. dorsalis*.

B, Boundary *H. f. fusciventris* vs. *H. f. lamtoensis*, and *Kassina cochranae* vs. *K. arboricola*.

C, Eastern limit for *H. f. burtoni*, and boundary *H. sylvaticus ivorensis* vs. *H. s. sylvaticus*.

D, Boundary *H. picturatus* vs. *H. baumanni*.

E, Dahomey Gap, where w and e represent the western and eastern border of the savanna gap boundary *H. s. sylvaticus* vs. *H. s. nigeriensis*, *H. c. concolor* vs. *H. c. ibadanensis*, and eastern boundary for *K. arboricola*.

F, Cross river: boundary *H. c. ibadanensis* vs. *H. c.* ssp., *L. hylondes* vs. *L. aubryi*, *H. f. burtoni* vs. *H. f.* ssp., and western limit for *H. bolifamba*e, *H. ocellatus*, *A. paradorsalis* and *H. kuligae*.

G, Sanaga river: southern limit for *H. fusciventris*, *H. sylvaticus* and *H. concolor*, north-western limit for *H. pardalis*, *H. platyceps* and *H. phantasticus*, northern limit for *Cryptothylax greshoffii* and south-eastern limit for *H. cameronensis*.

H, Boundary Cameroun-Rio Muni: boundary *A. d. dorsalis* vs. *A. d. regularis*, and *Phlyctimantis leonardi* vs. *P. boulengeri*.

I, Central Gabon.

J, Boundary Gabon-République du Congo: southern limit for *H. guttulatus*, *L. notatus* and *H. pardalis*.

K, Boundary République Democratique du Congo-Angola: southern known limit for *L. aubryi*, *H. phantasticus*, *H. adspersus* (?), *P. leonardi* and *C. greshoffii*, northern limit for *A. osorioi* along coast.

L, Southern limit for *A. dorsalis regularis* and probably *H. adspersus*.

M, Boundary *H. mitchelli* vs. *H. rubrovermiculatus*.

Source : MNHN, Paris

(2) A Central African fauna, from Cross river eastwards, different from the western fauna at species level. In the western part of the range, in the Cross-Sanaga forest and Congolian Coastal Forest ecosystem, this fauna is overlapping with the western fauna

(3) A distinct fauna in the Eastern Forests showing a total separation at species level from the remaining forests.

There is a considerable splitting up into subspecies, especially in the western fauna.

DISCUSSION

A pattern similar to the splitting up of the sylvicolous Hyperolidae into distinct insular faunas in discrete forest blocks is not seen among the parasylvicolous species. Instead, there is a considerable splitting up at places that appear "random" in the way that a clustering in groups of taxa sharing the same distribution seems to be lacking (fig. 8). This is especially apparent in the well-explored West Africa-Cameroun region and at the subspecific level in the most "versatile" genus, *Hyperolius*. In SCHIØTZ (1967), this "random" splitting up in West Africa was explained by the natural habitat, namely open, dry forest, being originally only found in a narrow belt, a forest edge at the well-defined forest-savanna border - plus in gallery forests stretching as tongues up into the savanna. Only when man disrupted the moist forest belt through farming and felling and thus created a network of open habitats, did large areas become suitable for the parasylvicolous fauna. Such an original, "linear" or "one-dimensional" distribution might facilitate taxonomic splitting up at rather insignificant and perhaps temporary barriers.

The westernmost part of West Africa (western Sierra Leone and adjacent parts of Guinea and Senegal) seems distinguished by the presence of the endemic *Hyperolius occidentalis*, as well as by the absence of the otherwise abundant and widespread species *Hyperolius concolor*, *H. picturatus* and *Afrixalus dorsalis*.

It is noteworthy that the two most distinct gaps for the sylvicolous faunas in West Africa are either not recognisable for the parasylvicolous fauna (V-baole) or rather unimportant (Dahomey Gap).

The Cross river is the western limit for several central African species, whereas a majority of the parasylvicolous species from West Africa continues along the Atlantic coast at least into Cameroun. The parasylvicolous fauna of the Cross-Sanaga and the Congolian Coastal Forests thus consists of two distinct fauna elements, a Central African mixed with a distinct West African element where no less than 5 out of the 8 parasylvicolous species of treefrogs occurring in Ghana are also found in remote Cameroun, including 4 out of 5 *Hyperolius*, a number tapering out when moving south from Cameroun along the coast. None of them are found inland in Central Africa. In comparison, none of the sylvicolous treefrogs from Ghana occurs in Cameroun.

Another element of parasylvicolous species is widely distributed in the Congo Basin but a closer analysis of the parasylvicolous fauna of central Africa is not possible with our present knowledge.

Source : MNHN, Paris

The Eastern Forest has a pattern of distribution different from the western forest blocks. The parasylvicolous fauna is widely distributed on suitable localities in the eastern lowlands as well as on the Eastern Arc. Contrary to the proposed "linear" or "one-dimensional" original distribution in West Africa, the original (i.e., before man transformed the landscapes) distribution of the parasylvicolous species in the eastern forest has been "two-dimensional", not confined to a narrow zone between moist forest and savanna, since the climax vegetation in the eastern forests has been large areas with a dry forest/savanna mosaic, habitable throughout by the parasylvicolous fauna. Of the parasylvicolous species in the eastern forests, only the species pair *Hyperolius mitchelli* vs. *H. rubrovermiculatus* (found respectively south and north of the Kenya-Tanzanian border) shows a pattern similar to that of West Africa with vicariant taxa replacing each other. Significantly this is where this eastern forest becomes a narrow "corridor" near its northern border, and a division there could be explained in the same way as the distribution pattern in West Africa (fig. 8).

POYNTON (1990) discussed the distinctness of the East African lowland fauna (below 300 m) and reached the conclusion that this fauna is not well defined or well delimited, but that nevertheless the lowland fauna has "a homogeneity which accords with the idea of a discrete 'fauna'" (p. 291). If his analysis (e.g., his figure 4) had included all the parasylvicolous frogs and had separated them from the savanicolous group, a much clearer pattern would have emerged with a distinct fauna found in the eastern lowlands, but generally penetrating higher up than the 300 m limit, into the parasylvicolous habitats in the Eastern Arc forests, apparently as high up as such habitats are found or explored (app. 4). Members of this fauna are here found to above 1000 m, sympatric with the sylvicolous fauna. West of the Eastern Arc mountains, the parasylvicolous fauna of block 10 seems to be absent, perhaps because of absence of the relevant habitats throughout the Arid Corridor.

POYNTON (1999: 485) found "endemism relatively low" in the East African lowlands. I claim, however, that endemism in the forest block here termed eastern forests is 100 %, not only for treefrogs, but also for other Amphibia. This apparently dramatic discrepancy is partly because Poynton limited his study to lowlands below 300 m, although a significant part of the fauna is found higher up, partly because I restrict my study to the parasylvicolous and sylvicolous faunas, omitting the numerous savanicolous species, many of which are found further inland.

THE MONTANE FAUNAS

Several families of Anura have a strong element of orophile, forest-related species and genera. In many cases the tadpoles are adapted to swift-flowing streams, and the species could be termed rheophile rather than orophile. No rheophile treefrogs are known, and an orophile element in this group is ill-defined and seems weak. A number of species are only or predominantly found above 1000-1500 m and are often regarded as montane, but it can be argued that there are few real montane species among the treefrogs since most species can be found as far down as suitable vegetation is found, to 100-200 m. Therefore no attempt has been made to distinguish the montane species as a special category in this study.

Source : MNHN, Paris

The "montane" species in the tropical forest belt are found in three areas, namely mount Cameroun and the Cameronese ridge, the Albertine rift mountains including the Itombwe plateau, and finally the Eastern Arc mountains. The "montane" treefrog faunas in these three areas are separate from each other at species level. The best developed orophile element is found in the Albertine rift montane areas with a number of species known only from high altitude (see block 9, p. 16). In the Eastern Arc mountains, a few species are known only from altitude above 1000 m but they are all species known from so few localities that a realistic assessment of their altitudinal distribution is uncertain (app. 4, discussion p. 19). In the Cameronese ridge only one treefrog, *Afrixalus lacteus*, is confined to high altitude, the remaining treefrogs from this area can occasionally be found at low altitude (AMIET, in litt.). The well-investigated mount Nimba (1750 m) in West Africa has no orophile treefrogs.

CONCLUSION

THE HISTORY OF THE SYLVICOLOUS AND PARASYLVICOLOUS FAUNAS

In SCHIØTZ (1967), it was postulated that the distribution pattern of the West African sylvicolous treefrogs could be explained fully from the vicissitudes in late Pleistocene, during which the last arid period has divided the forest into isolated islands for sufficiently long periods to allow the most versatile genus, *Hyperolius*, to develop discrete species, while the more conservative genera *Afrixalus* and *Leptopelis* did not show a splitting up on either side of V-baole, but a distinct break at the species level at the Dahomey Gap. The most conservative genera *Chiromantis*, *Bufo* and *Ptychadena* show only limited division between West Africa and Central Africa. There are thus three "levels" of species diversification for the sylvicole Amphibia (fig. 3-5)

The relevant factors seem to be climatic fluctuations resulting in vegetational fluctuations during the latter part of Pleistocene, over approximately the last 40,000 years (TINSLEY et al., 1996, MALEY, 1996): a cold and arid period from 40,000 to 12,000 years before present (ybp) resulted in the lowland forest retracting considerably, to be partly replaced by savanna. Most extreme aridity occurred from about 25,000 to about 12,000 ybp, during the glacial maxima in the northern hemisphere. There is, however, extensive evidence that lowland rainforest persisted in a number of refugia determined by local conditions of altitude, precipitation and soil type. The most common state in the upper Pleistocene would be a relatively fragmented forest mass, but with larger areas of forest than those postulated for the most arid phase.

The end of the last glaciation was characterised by a rapid rise in temperature approximately 12,000 years ago. The lowland tropical forest expanded, reaching a maximum circa 7,000 ybp, a maximum which, however, did not unite the Central African forests with those of the Eastern Arc.

It is suggested (MALEY, 1996) that in the last major arid phase (circa 18 000 ybp) forest refugia persisted as two or three areas in West Africa, one in the Cross-Sanaga forest, four refugia in the Congolian Coastal forest, one large refugium along Congo river, another along the Albertine rift and finally a number of small refugia in the Eastern Arc mountains (fig. 9). COLYN et al. (1991) suggested a more complicated pattern for the Congo Basin.

Source : MNHN, Paris

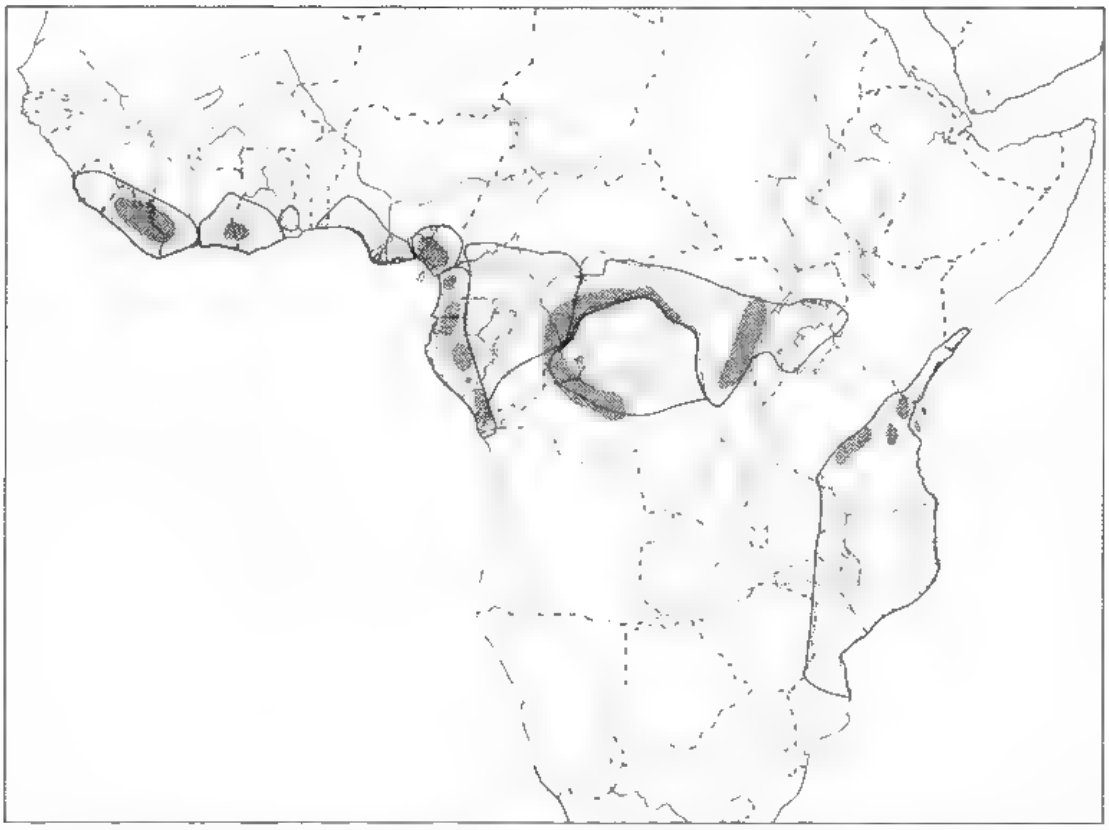


Fig 9 – Proposed dry-period forest refugia. Redrawn after MALEY (1996), with a small refugium added at mount Doudou, Gabon, as proposed by SOSEF (1994). Also added are the Eastern Forests.

Based on the proposed forest refugia, one can explain the distinctness of blocks 1 and 2, and 5 and the northern part of 6, whereas the southern part of 6, south of Cameroun, and of 7, 8 and 9 are not well collected enough to allow drawing conclusions. Therefore the four or five refugia suggested (MALEY, 1996) from Equatorial Guinea (Rio Muni) to Mayombe cannot with our present knowledge be substantiated through the distribution of the treefrogs, although we have collections from localities situated at or very close to all of them.

The three ecoregions in the Congo Basin seem, with our present knowledge, to have a very similar lowland fauna. Whether the small differences between the three blocks point at three discrete regions with the Congo and Ubangi rivers as borders, or gradual changes in the huge Congo basin is not known. Three well-defined regions with clear borders, as suggested by WWF's divisions into ecoregions, would seem unlikely since drier periods in Pleistocene probably never split the Congo Basin forest up into three refugia separated by the river, a situation of Congo basin refugia as indicated in fig. 9 would seem rather more likely.

Data for primates supported by plants (COLYN et al., 1991) seem to point at faunal breaks in the Congo basin originating from several nuclear areas on both sides of the Congo-Lualaba river, suggesting that, during the last arid period, populations survived in several refugia

Source : MNHN, Paris

within the Congo basin. Zones of intergradation strongly suggest that dispersal operated from these areas and not only from the Albertine rift and from the West Central (Cameroun-Gabon) refugia.

Block 10 shows no sign of having been connected with the rest of the blocks, with no species in common.

It is difficult to say whether the occurrence of several small genera of Hyperoliidae in Cameroun is caused by a refugium there having persisted even longer back in time, or by the forests there having been consistently wetter and thus more favourable for frogs and their diversification, or on the perseverance of herpetological scrutiny.

The forest in the Congo basin is frequently described in the literature as species-poor, a poverty explained by it being a young forest as shown by it standing on Kalahari sand. Thus FAIRBRIDGE (1968) wrote: "almost the whole Congo basin was invaded by dune sands from the Kalahari during the period 50 000-10.000 B.P", and many other authors supported this idea. WHITE (1993) rejected this theory and suggested it was based on confusion between "Kalahari sands" and the "Kalahari geological system" According to White, the sand dunes and formations are nowhere approaching the equator, and the forest in the central Congo basin is not particularly young

The theory that refugia in the lowland forests has acted as evolutionary centres was challenged by FJELDSÅ & LOVETT (1997) Based on birds and some plant families in forest biota, where the authors distinguished between old and young species, they did not find strong evidence for the importance of Pleistocene refugia as centres for allopatric speciation They saw the refugia rather as "museums", maintaining old species, and demonstrated that "the proliferation of young species takes place mainly at the periphery of the main rainforest blocks" The data for sylvicolous treefrogs, meagre when they are compared to birds and plants, might add arguments to this discussion. For most genera of Amphibia among the treefrogs *Leptopelis* and *Afrixalus* the refugia can be seen as museums, carrying sets of species through periods of forest division, but for *Hyperolius* the rule seems to be that each major, well-investigated forest block which has harboured a refugium has developed its own set of sylvicolous *Hyperolius* An explanation could be that the genus *Hyperolius* is more "versatile" so that the rather brief periods of isolation of the refugia have been sufficient for these refugia to act as evolutionary centres. *Hyperolius* would thus according to Fjeldså & Lovett's term be composed of "young species" The considerable subspecific splitting up of the parasylvicolous treefrogs compared to the sylvicolous may suggest the parasylvicolous taxa to be younger than the sylvicolous. The diversification of the parasylvicolous species, apparently unrelated to former forest refugia, seems to have taken place at "the periphery of the forest belt", namely along the original forest-savanna border (present paper, p. 15) Data for diversity of treefrogs (SCHIOTZ, 1999, fig 2) using WorldMap as basis for analysis, apparently support the view of Fjeldså & Lovett by showing a peak of diversity in the periphery of the forest belt, most conspicuous in the well-investigated West Africa A closer analysis of the data for treefrogs shows, however, that this is solely caused by an increased habitat diversity in the forest-savanna transition zone within the rather coarse 110 × 110 km grids used by WorldMap, where the sylvicolous, parasylvicolous and savanicolous faunas are superimposed None of these three faunas becomes more diverse here, understood as richer in species or subspecies, but all three faunas are present within a grid, as different from the

Source : MNHN, Paris

condition further away from the transition zone. This comment is not relevant to Fjeldså & Lovett's own conclusions since they deal only with forest-related species.

In strong contrast to the explanation presented here of the present distribution pattern being explicable by climate fluctuations in late Pleistocene and *Hyperolius* being a genus of young species, WIECZOREK et al. (2000) postulated a far longer history for the diversification in the genus *Hyperolius*. Their thesis is based on mtDNA sequence data, habitat preference and current distribution. By referring each node in their dendrogram, based on mtDNA (p. 1237), to a distinct geological, climatic and vegetation change – without making it clear why each step on their dendrogram necessarily corresponds with one step on their list of palaeoenvironmental changes – they claim that they can trace the species diversification in the genus *Hyperolius* back to Cretaceous and Palaeocene. An assessment of their theory is difficult since both their distribution maps and their references to habitat preference are unconventional. The authors thus work with habitat preferences savanna, forest and generalists. The latter term is not explained. If the term generalist refers to what is here termed parasylvicolous I do question the correctness. The parasylvicolous fauna does not seem more generalised in its habitat choice than the sylvicolous and savanicolous, and the 6 species referred to that category in their paper do not clarify matters since it refers to 2 montane sylvicolous species, 2 parasylvicolous and 2 savanicolous, whereas all their "forest species" are parasylvicolous in my terminology. Rather than giving distribution maps based on collected specimens, their distribution is "extrapolated taking into account. habitat utilisation". But since their allocation to habitat utilisation is most unconventional – and unexplained in the text – so are the resulting distribution maps.

A theory of theirs is that the genus *Hyperolius* originated as generalists and became increasingly specialised in terms of habitat. Strangely their only supporting argument, *Hyperolius cinnamomeoventris*, which is both the basal lineage on the dendrogram and the only suspected generalist in the genus (apparently being both parasylvicolous and savanicolous, unless it is a composite of several species), is termed in their paper as a forest species and would thus seem to contradict their thesis. Unfortunately no sylvicolous species from lowland forests is included in their study. Bringing species diversification in *Hyperolius* back to Cretaceous would make this genus the oldest African frog genus together with *Xenopus*. Not until Miocene do we have records of other families than Pipidae (DUELLMAN, 1993). The latest diversification in their dendrogram on p. 1237 is during "Pleiocene" (Pliocene or Pleistocene?) but seems only to have influenced speciation in the superspecies *Hyperolius viridiflavus*, a group of very closely related savanicolous taxa.

I doubt whether the present species structure in *Hyperolius* has its rooting back in Cretaceous, 70 million years ago. I feel that *Hyperolius* shows many signs of being a very new genus, more in the process of rapid, recent speciation than most or all other African genera of Amphibia. I feel that the species pattern in the genus *Hyperolius* can be fully explained as the result of climatic and vegetation changes during late Pleistocene, a period of approximately 35,000 years.

Source : MNHN, Paris

ACKNOWLEDGEMENTS

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Source : MNHN, Paris

Appendix 1

List of taxa mentioned in this paper, according to the familial and generic taxonomy of Frost et al. (2006)

Genus	Species and subspecies
Family *Hyperoliidae* Laurent, 1943	
Acanthixalus Laurent, 1944	*sonjae* Rödel, Kosuch, Veith & Ernst, 2003, *spinosus* (Buchholz & Peters, 1875)
Afrixalus Laurent, 1944	*dorsalis dorsalis* (Peters, 1875); *dorsalis regularis* Laurent, 1951, *equatorialis* (Laurent, 1941); *fulvovittatus* (Cope, 1861); *lacteus* Perret, 1976, *laevis* (Ahl, 1930); *leucostictus* Laurent, 1950; *nigeriensis* Schiøtz, 1963, *osorioi* (Ferreira, 1906), *paradorsalis* Perret, 1960; *schneideri* (Boettger, 1889); *sylvaticus* Schiøtz, 1974; *uluguruensis* (Barbour & Loveridge, 1948); *vibekensis* Schiøtz, 1967
Alexteroon Perret, 1988	*hypsiphonus* Amiet, 2000; *pinx* Amiet, 2000, *obstetricans* (Ahl, 1931)
Arlequinus Perret, 1988	*krebsi* (Mertens, 1938)
Callixalus Laurent, 1950	*pictus* Laurent, 1950
Chlorolius Perret, 1988	*koehleri* (Mertens, 1940)
Cryptothylax Laurent & Combaz, 1950	*greshoffii* (Schilthuis, 1889), *minutus* Laurent, 1976
Hyperolius Rapp, 1842	*acutirostris* Buchholz & Peters, 1875, *adspersus* Peters, 1877, *alticola* Ahl, 1931; *baumanni* Ahl, 1931, *bohirensis* Schiøtz, 1967; *bolifambae* (Mertens, 1938); *bopeleti* Amiet, 1980, *brachiofasciatus* Ahl, 1931, *camerunensis* Amiet, 2004, *castaneus* Ahl, 1931; *chlorosteus* (Boulenger, 1915); *chrysogaster* Laurent, 1950; *cinnamomeoventris* Bocage, 1866, *concolor concolor* (Hallowell, 1844); *concolor ibadanensis* Schiøtz, 1967, *diaphanus* Laurent, 1972, *dintelmanni* Lötters & Schmitz, 2004; *endjami* Amiet, 1980; *ferrugineus* Laurent, 1943; *frontalis* Laurent, 1950; *fusciventris burtoni* (Boulenger, 1883), *fusciventris fusciventris* Peters, 1876, *fusciventris lamtoensis* Schiøtz, 1967, *ghesquieri* Laurent, 1943; *guttulatus* Günther, 1858, *hutsebauti* Laurent, 1956; *inornatus* Laurent, 1943, *kihangensis* Schiøtz & Westergaard, 1999, *kivuensis* Ahl, 1931, *kuligae* Mertens, 1940, *langi* Noble, 1924, *lateralis* Laurent, 1940, *laurenti* Schiøtz, 1967; *leleupi* Laurent, 1951, *leucotaenius* Laurent, 1950; *mitchelli* Loveridge, 1953, *mosaicus* Perret, 1959, *nasutus* Günther, 1865, *nienokouensis* (Rödel, 1998); *nimbae* Laurent, 1958, *occidentalis* Schiøtz, 1967, *ocellatus* Günther, 1858, *pardalis* Laurent, 1948, *phantasticus* (Boulenger, 1899); *picturatus* Peters, 1875; *platyceps* (Boulenger, 1900), *puncticulatus* (Pfeffer, 1893), *riggenbachi hieroglyphicus* Ahl, 1931, *riggenbachi riggenbachi* (Nieden, 1910); *robustus* Laurent, 1979, *rubrovermiculatus* Schiøtz, 1975, *sankuruensis* Laurent, 1979, *spinigularis* Stevens, 1971, *sylvaticus ivorensis* Schiøtz, 1967; *sylvaticus nigeriensis* Schiøtz, 1967, *sylvaticus sylvaticus* Schiøtz, 1967, *tannerorum* Schiøtz, 1982, *torrentis* Schiøtz, 1967, *tuberculatus* (Mocquard, 1897), *viridiflavus* (Duméril & Bibron, 1841); *viridigulosus* Schiøtz, 1967, *wermuthi* Laurent, 1961, *xenorhinus* Laurent, 1972, *zonatus* Laurent, 1958
Kassina Girard, 1853	*arborticola* Perret, 1985, *cochranae* (Loveridge, 1941); *decorata* (Angel, 1940); *lamottei* Schiøtz, 1967; *maculosa* (Sternfeld, 1917), *mertensi* Laurent, 1952, *schioetzi* Rödel, Grafe, Rudolf & Ernst, 2002
Opisthothylax Perret, 1966	*immaculatus* (Boulenger, 1903)
Phlyctimantis Laurent & Combaz, 1950	*boulengeri* Perret, 1986; *keithae* Schiøtz, 1975, *leonardi* (Boulenger, 1906), *verrucosus* (Boulenger, 1912)

Source : MNHN, Paris

APPENDIX 1 (continued)

Genus	Species and subspecies
Family *ARTHROLEPTIDAE* Mivart, 1869	
Arthroleptis Smith, 1849	
Astylosternus Werner, 1898	*batesi* (Boulenger, 1900); *diadematus* Werner, 1898
Cardioglossa Boulenger, 1900	*gratiosa* Amiet, 1972, *nigromaculata* Nieden, 1908
Leptodactylodon Andersson, 1903	*albiventris albiventris* (Boulenger, 1905), *albiventris bueanus* Amiet, 1981, *ovatus* Andersson, 1903, *ventrimarmoratus* (Boulenger, 1904)
Leptopelis Günther, 1859	*aubryi* (Dumeril, 1856); *barbouri* Ahl, 1929, *boulengeri* (Werner, 1898); *brevirostris* (Werner, 1898); *calcaratus calcaratus* (Boulenger, 1906); *calcaratus meridionalis* Laurent, 1973; *christyi* (Boulenger, 1912); *crystallinoron* Lötters, Rödel & Burger, 2005, *fenestratus* Laurent, 1972; *fiziensis* Laurent, 1973, *flavomaculatus* (Günther, 1864), *hyloides* (Boulenger, 1906); *kivuensis* Ahl, 1929, *mackayi* Köhler, Bwong, Schick, Veith & Lötters, 2006, *macrotis* Schiøtz, 1967, *millsoni* (Boulenger, 1895), *modestus* (Werner, 1898); *notatus* (Peters, 1875), *occidentalis* Schiøtz, 1967, *ocellatus ocellatus* (Mocquard, 1902), *ocellatus schiøtzi* Laurent, 1973; *omissus* Amiet, 1992; *parkeri* Barbour & Loveridge, 1928, *rufus* Reichenow, 1874; *uluguruensis* Barbour & Loveridge, 1928; *vermiculatus* (Boulenger, 1909); *zebra* Amiet, 2001
Family *BUFONIDAE* Gray, 1828	
Bufo Laurenti, 1768	-
Family *PIPIDAE* Gray, 1828	
Xenopus Wagler, 1827	-
Family *PTYCHADENIDAE* Dubois, 1987	
Ptychadena Boulenger, 1917	-
Family *PHRYNOBATRACHIDAE* Laurent, 1941	
Phrynobatrachus Günther, 1862	-
Family *RHACOPHORIDAE* Hoffman, 1932 (1858)	
Chiromantis Peters, 1854	*rufescens* (Günther, 1869)

APPENDIX 2

COMPARISON OF TERMINOLOGY BETWEEN THIS PAPER, WWF'S GLOBAL 200 (OLSON & DINERSTEIN, 1998) AND POYNTON (1999)

Present treatment	Global 200	POYNTON, 1999
Liberia (block 1) + Gold Coast (block 2) + Trans-Volta -Togo (block 3)	Guinean Moist Forests	Western province of West Equatorial Region
Southern Nigeria (block 4)	No separate ecoregion	Central, East and South Province of West Equatorial Region Not congruent with subdivisions of WWF
Cross-Sanaga Coastal Forests (block 5)	Northwestern part of Congolian Coastal Forests	
Congolian Coastal Forests (block 6)	Southern part of Congolian Coastal Forest	
North-western Congolian Forests (block 7)	Western Congo Basin Moist Forests	
Central Congolian Forests (block 8)	Central Congo Basin Moist Forests	
North-eastern Congolian Forests (block 9)	North-eastern Congo Basin Moist Forests	
Eastern Forests (block 10)	Eastern Arc Montane Forests + East African Coastal Forests	Eastern province of Intertropical Montane Region + East Coast Forests + Forested parts of eastern Coast Lowlands

Source : MNHN, Paris

APPENDIX 3

NOTES ON PROBLEMATIC SPECIES

A number of treefrogs, especially from Central Africa, have unknown habitat preferences and are therefore omitted here. They are *Cryptothylax minutus*, *Hyperolius brachiofasciatus*, *H. chrysogaster*, *H. diaphanus*, *H. ferrugineus*, *H. mornatus*, *H. leucotaenius*, *H. sankuruensis*, *H. xenorhinus* and *Leptopelis fenestratus*.

A group of treefrogs seems to prefer habitats which are intermediary between sylvicolous and parasylvicolous, and reference to either of these categories can be disputed. It is my impression that such species do not generally have broader habitat requirements, being more generalised than others, but are rather "in between", preferring dense vegetation in parasylvicolous habitats or open vegetation in sylvicolous habitats. *Hyperolius sylvaticus*, *Kassina cochranae*, *K. arboricola* and *Phlyctimantis boulengeri* were with reservations referred to as sylvicolous by SCHIOTZ (1967). Here, partly based on the extensive field knowledge of RÖDEL (in litt.), they are termed parasylvicolous although found in denser vegetation in this habitat type. Similarly, AMIET (1986) has listed *Acanthixalus spinosus*, *Afrixalus paradorsalis*, *Hyperolius kuligae*, *H. ocellatus* and *H. platyceps* as occasionally occurring in both habitats. The preferred habitat is used here.

The so-called *Afrixalus fulvovittatus* group (SCHIOTZ, 1999) (striped *Afrixalus*) has an unsettled and confused taxonomy, probably consisting of several species, some savanicolous, others parasylvicolous. The parasylvicolous form in western West Africa (*A. fulvovittatus* sensu stricto) seems well defined in westernmost Africa, but RODEL et al. (2005) mentioned the possible occurrence of this species in south-western Ghana. RODEL & PICKERSGILL (in litt.), however, raised doubts about the identity of the eastern samples. A photo by Leache sent to me by Pickersgill (from Ankassa, Ghana) is of *A. dorsalis* with a middorsal stripe. In Cameroun and Central Africa the situation is unsettled. This complex is disregarded here.

Afrixalus schneideri is an enigmatic species with a characteristic morphology which could indicate that it is the Cameronese representative of a group of large sylvicolous *Afrixalus* including *A. equatorialis*, *A. leucostictus* and *A. nigeriensis*, but only one specimen is known, from a very well explored part of Cameroun.

Hyperolius spinigularis has an enigmatic habitat preference, being apparently found both in dense forest and in very open farmland, but so inconspicuous and therefore easily overlooked that distribution cannot be given. Most records are above 1000 m. The species is omitted in this study.

Hyperolius langi is omitted since its habitat preference and taxonomy are badly understood especially in relation to *H. kuligae* and *H. platyceps*. Doubtful records from Uganda (SCHIOTZ, 1999, as *H. kuligae*) may be *H. langi*.

Hyperolius cinnamomeoventris is the only *Hyperolius* assumed to be both parasylvicolous and savanicolous. Only parasylvicolous populations are dealt with here, as this name might possibly cover several species.

Spotted *Kassina* from forest regions form a parasylvicolous group with an unsettled taxonomy. In West Africa, RODEL et al. (2002) revised the group, and two members, *K. arboricola* and *K. cochranae* are included in this study. The third West African species, *K. schioetzi*, is omitted because of uncertainty about its habitat affinity. Further east the situation is unsettled. In the well investigated Cameroun, several taxa seem to be confused under the name *K. maculosa* or *K. decorata*. Further east, available material is insufficient. The spotted forest kassinas from Central Africa are therefore omitted.

Leptopelis modestus has a doubtful taxonomy. Possibly four taxa are involved: from Cameroun possibly two taxa with slightly different morphologies, from montane forests (eastern Nigeria and western Cameroun) and lowland forests (the latter harbouring the type locality), furthermore recorded from eastern Congo and from western Kenya, the latter population having recently been described as *L.*

Source : MNHN, Paris

mackayi Only the Cameronese populations of *L. modestus* and *L. mackayi* are treated here, the eastern Congo populations omitted

Phlyctimantis boulengeri occurs in the Liberia block and in the westernmost Gold Coast block, and then, after a hiatus of 1000 km, in easternmost Nigeria and in Cameroun Being a conspicuous species, it was probably not overlooked in between There is suspicion that the two populations, "*P boulengeri* W" and "*P boulengeri* E" are two different taxa (RÖDEL & ERNST 2001, SCHIOTZ, 1999), therefore the two populations are treated here as separate taxa.

APPENDIX 4

ALTITUDINAL RANGES OF SPECIES IN BLOCK 10

Data were kindly provided by POYNTON (in litt) and supplemented with my own data

200 m is the lowest investigated altitude with closed canopy moist forest (east slopes of Eastern Usambaras)

PARASYLVICOLOUS SPECIES

Hyperolius mitchelli 10-1050 m
Hyperolius puncticulatus: 10-2100 m
Leptopelis flavomaculatus : 10-1370 m
Phlyctimantis keithae: 1840-1950 m.

SYLVICOLOUS SPECIES

Afrixalus uluguruensis : 750-1740 m.
Hyperolius kihangensis: 1410 m.
Hyperolius tannerorum: 1740 m.
Leptopelis barbouri: 1000-1740 m.
Leptopelis parkeri: 410-1740 m
Leptopelis uluguruensis: 200-1250 m
Leptopelis vermiculatus: 200-1410 m

Source : MNHN, Paris

Alytes, 2007, **25** (1-2): 38-44.

Defensive behaviour with stiff-legged posture in the Brazilian tree toads *Dendrophryniscus brevipollicatus* and *D. leucomystax* (Anura, Bufonidae)

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We observed death feigning with stiff-legged posture in several individuals of the Brazilian tree toads *Dendrophryniscus brevipollicatus* and *D. leucomystax*. This behaviour was formerly described for three other phylogenetically unrelated Brazilian leaf-litter frogs. Besides their cryptic colouration, tonic immobility during this posture strongly enhances the resemblance of these anurans to fallen leaves on the forest floor. This behaviour seems to have evolved independently in different lineages as a very effective defensive mechanism against visually oriented predators, especially vertebrates.

INTRODUCTION

Death feigning, or tonic immobility or thanatosis, as an anti-predator behaviour arose independently in several animal lineages. In neotropical frogs, death feigning was already reported in species belonging to the families Bufonidae (HADDAD & SAZIMA, 1992, ABBADIE-BISOGNO et al., 2001; RUSSELL, 2002, TOLEDO, 2004, VAZ-SILVA & FROTA, 2004), Cycloramphidae (SAZIMA, 1978), Dendrobatidae (VAZ-SILVA & FROTA, 2004), Hylidae (SAZIMA, 1974, DUELLMAN & TRUEB, 1994, AZEVEDO RAMOS, 1995, VRCIBRADIC & VAN SLUYS, 2000, GOMES et al., 2002), Microhylidae (SAZIMA, 1978, VAZ-SILVA & FROTA, 2004) and Rhinodermatidae (POUGH et al., 2004). Death feigning with stiff legged posture, however, was described only for three cryptically coloured leaf litter frogs: the microhylid *Stereocyclops parkeri* (Wettstein, 1934), the cycloramphid *Proceratophrys appendiculata* (Gunther, 1873) (SAZIMA, 1978) and the leptodactylid *Scythrophrys sawayae* (Cochran, 1953) (GARCIA, 1999).

Source : MNHN, Paris

Here we describe death feigning with stiff-legged posture in the Brazilian tree toads *Dendrophryniscus brevipollicatus* Jiménez de la Espada, 1871 and *D. leucomystax* Izecksohn, 1968 (Bufonidae) from three localities in the states of São Paulo and Santa Catarina, southeastern and southern Brazil.

MATERIAL AND METHODS

Dendrophryniscus brevipollicatus is a small toad (snout-vent length [SVL] ♂ 14.5 mm, ♀ 19.3 mm; HEYER et al., 1990) known from the coastal ranges of southeastern Brazil (HEYER et al., 1990; IZECKSOHN & CARVALHO-E-SILVA, 2001). This species is easily diagnosed by its small size, a pointed-mucronate dorsal snout shape, and reduced thumbs (HEYER et al., 1990). According to HEYER et al. (1990), it is apparently active on the forest floor during the day, resting on leaves above the ground at night. It is strongly associated to terrestrial bromeliads, where their eggs are laid and tadpoles develop (CARVALHO, 1949, LUTZ, 1954; PEIXOTO, 1995).

Dendrophryniscus leucomystax superficially differs from *D. brevipollicatus* by the presence of a white stripe extending from snout tip to base of arms, but several other differences distinguish these two similar toadlets (IZECKSOHN, 1968). The species is known from the lowland coastal forests of southeastern and southern Brazil (IZECKSOHN, 1968; WOLHL & WOEHL, 2006). It is a small toad (SVL ♂ 21.0 mm, ♀ 25.0 mm, IZECKSOHN, 1968) that is found in secondary and primary forests on leaves near the ground, including terrestrial bromeliads, and on the forest floor (IZECKSOHN, 1968, pers. obs.). Eggs are laid in temporary puddles on the forest floor, where tadpoles develop and attain metamorphosis (IZECKSOHN & CRUZ, 1972).

One individual of each species from localities in the state of São Paulo was collected, killed in a CO_2 artificial atmosphere, preserved in 10 % formalin and housed in the herpetological collection of the Laboratório de Zoologia de Vertebrados, Departamento de Ciências Biológicas, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Brazil (field numbers IC 012 and CB 002). Voucher specimens (colour transparencies) from the state of Santa Catarina are housed in the herpetological collection of the Kansas University, Lawrence, USA (KU-CT 11954–11957).

STUDY SITES

Observations were made in three sites belonging to the Atlantic Rainforest Morphoclimatic Domain (AB'SABER, 1977), southern and southeastern Brazil, as follows.

(1) The Parque Estadual Carlos Botelho (PECB) is a 37793 ha reserve of well-preserved Atlantic rainforest located in the municipality of Sete Barras, state of São Paulo, southeastern Brazil (24°00'-24°15'S, 47°45'-48°10'W). Altitudes vary from 30 to 1003 m (DOMINGUES & SILVA, 1988). In the area where our observations were made, climate is Cfb of Koeppen, with the mean temperature of the warmest month not superior to 22°C (SETZER, 1946).

Source : MNHN, Paris

(2) The Parque Estadual da Ilha do Cardoso (PEIC) is a 22,500 ha island located in municipality of Cananeia, state of São Paulo, southeastern Brazil (25°03'-25°18'S, 47°53'-48°05'W) For the period 1990-1991, the minimum daily temperatures averaged 19°C and the maximum daily temperatures averaged 27°C, and the annual rainfall varied between 1800 and 2000 mm (MELO & MANTOVANI, 1994). Altitudes vary from sea level to 800 m. Our observations were made almost at sea level in a well-preserved dense Restinga.

(3) The third site is a well-preserved dense Restinga fragment located in Quati, municipality of Guaramirim, state of Santa Catarina, southern Brazil (26°26'S, 48°57'W). Observations were made at 10m above sea level. Mean annual rainfall between 2002 and 2005 was 1900 mm Climate is subtropical, with mean annual air temperature around 20°C (ANONYMOUS, 1997).

RESULTS

DENDROPHRYNISCUS BREVIPOLLICATUS

On October 8th, 2005, we observed death feigning in two individuals of *D brevipollicatus* in PECB. At 12 11 h, one individual (SVL 17.5 mm) defended itself stiffing its legs in response to hand capture The same behaviour was observed in another individual (13 7 mm) at 17 05 h (fig 1a). We then gently rolled the toadlet around its longitudinal axis, simulating a bird beak with a finger, and observed that it remained immobile in its rigid posture (fig. 1b).

At the same site, on June 10th, 2006, four individuals displayed stiff-legged defensive behaviour At 12 10 h one individual (SVL 15 4 mm) after disturbation maintained the rigid posture for almost five minutes. At 12 47 h one individual (16.8 mm) defended itself in response to searcher moving At 14 42 h another individual (16.5 mm) feigned death several times following manipulation At 21 10 h a female apparently bearing eggs (SVL 21 0 mm) adopted the stiff-legged posture

DENDROPHRYNISCUS LEUCOMYSTAX

On July 9th, 2002, around 15 00 h, death-feigning was displayed by an adult *D leucomystax* (SVL 16 mm) in Guaramirim Restinga fragment When the animal was put upside down to be photographed, it remained in thanatosis posture (fig. 1c) On July 27th, 2002, between 14 00 and 17 00 h, at the same site, another individual (SVL 14 mm) was found on the leaf-litter and assumed the typical stiff legged defensive posture when touched by the searcher, remaining immobile for almost 1 minute (fig 1d) Snout-vent length for the individuals (juveniles and adult males and females) sampled in this fragment varied from 14 to 22 mm (mean 17 ± 2 mm; $n = 29$).

On September 4th, 2005, death-feigning was displayed during the day (12 11 h) by an adult *D leucomystax* in a Restinga area of the PEIC After hand capture for identification, the toad was put upside down to take photographs of its ventral surface It remained motionless

Source : MNHN, Paris

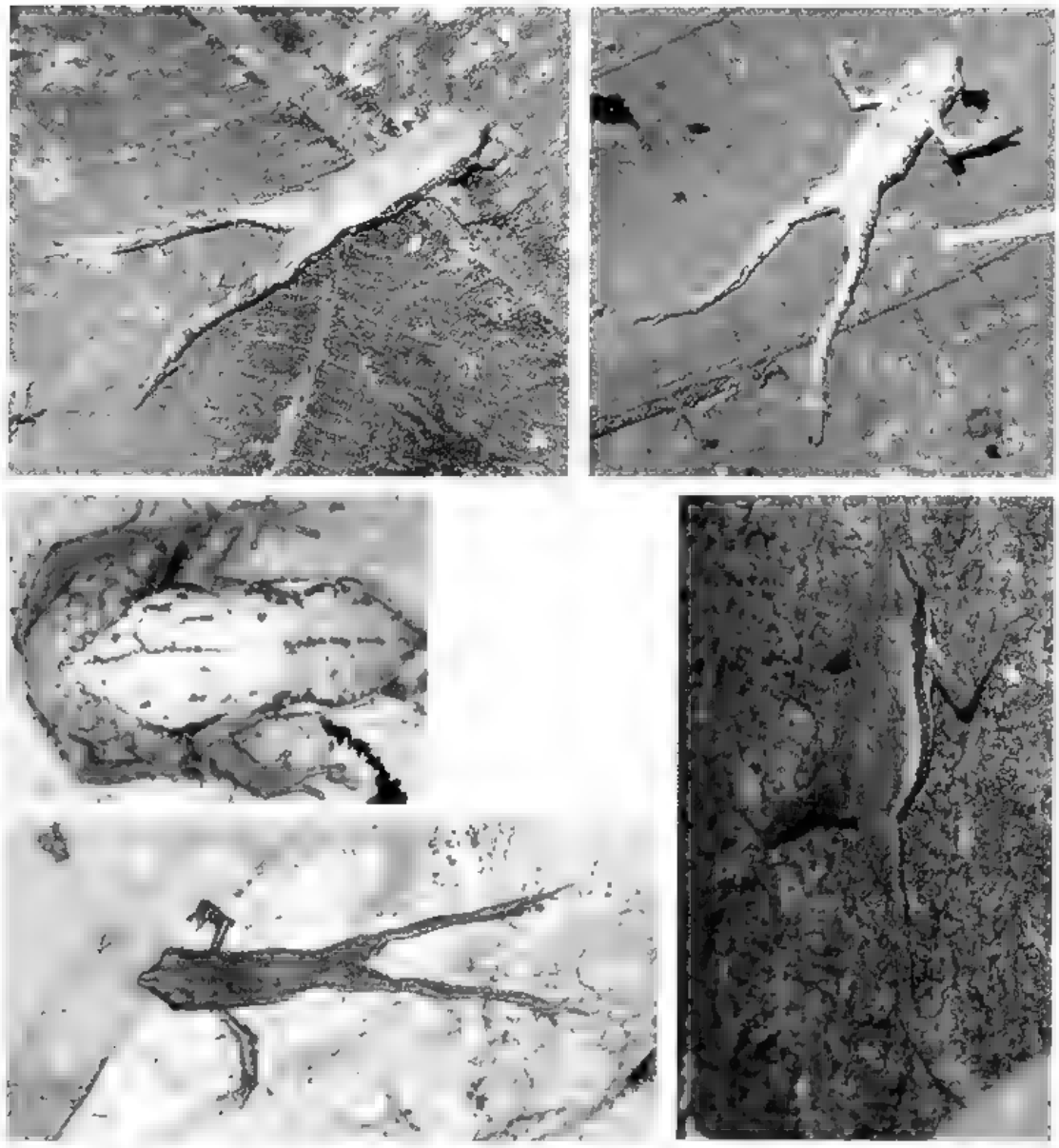

Fig. 1. Death feigning in the Brazilian tree toads *Dendrophryniscus brevipalliatus* (a-b) and *D. leucomystax* (c-e).

in a death feigning-like posture with eyes opened. We then caught the toad again and it leaped and landed on a leaf of a terrestrial bromeliad with the legs stretched backwards, remaining motionless and with eyes opened. The toad was photographed but not collected. On November 6th, 2005, at the same site, death-feigning by another adult *D. leucomystax* was observed during the day (17:39 h). After hand capture, the toad leaped and landed on a tree trunk, where it assumed the stiff-legged posture (fig. 1e). Two additional observations of this behaviour were made in 2006, on January 10th (09:42 h) and February 4th (15:33 h).

Source : MNHN, Paris

Discussion

Besides their cryptic colouration, the stiff-legged posture adopted by these toadlets greatly enhances their resemblance to fallen leaves both in colour and shape. As pointed out by Sazima (1978) for *Proceratophrys appendiculata* and *Stereocyclops parkeri*, tonic immobility in these cases may cause an animal to be confused with a casually dislodged leaf. This is suggested by the result of our simple experiment of rolling the animal around its axis. This defensive strategy may protect the individual against visually oriented predators like birds, snakes and mammals that actively search for their prey in the leaf-litter. The maintenance of the rigid posture for rather long periods – almost five minutes in *Dendrophryniscus brevipollicatus* and up to 10 minutes in *Scythrophrys sawayae* (Garcia, 1999) – suggests that this behaviour was selected against visually oriented predators. Similar predatory pressures on the forest floor possibly resulted in the convergent behavioural patterns observed in several unrelated frogs (Sazima, 1978). The instinctiveness of this behaviour is suggested by its being triggered and maintained in different species even in unexpected situations, like while submerged (Garcia, 1999) or vertically positioned on a tree trunk, or at night (this paper).

The related *Dendrophryniscus minutus* from the Amazonian region of South America also displays death feigning, but in a very different way. When captured, this toad flips over on its back and remains motionless in dorsal recumbency with the legs held upward. This posture makes evident the bright orange path on its venter and its orange palms and soles, thus consisting in a defensive behaviour associated to aposematism (Russell, 2002). Venter, palms and soles of *D. brevipollicatus* and *D. leucomystax* (fig. 1b-c) and of *Scythrophrys sawayae* (Garcia, 1999) do not have such warning colours, so these species did not evolve an aposematic behaviour similar to *D. minutus*. Thanatosis in dorsal recumbency, however, seems to be a common (probably primitive) defense strategy, since it was displayed by almost all individuals in different species and lineages that display stiff-legged posture.

Résumé

Une attitude de mort feinte, avec les pattes postérieures raides, a été observée chez plusieurs individus des Bufonidés brésiliens *Dendrophryniscus brevipollicatus* et *D. leucomystax* dans trois localités du sud et sud-est de Brésil. Ce comportement avait déjà été décrit pour trois autres anoures brésiliens non directement apparentés. Associée à leur coloration cryptique, cette immobilité tonique renforce la ressemblance de ces anoures avec des feuilles mortes tombées sur la litière forestière. Ce comportement semble avoir évolué d'une manière indépendante dans des lignées différentes comme un mécanisme défensif très efficace contre les prédateurs, notamment des Vertébrés qui effectuent une recherche visuelle des proies.

Source : MNHN, Paris

ACKNOWLEDGEMENTS

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The tadpole of *Eupsophus queulensis* (Anura, Cycloramphidae)

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The genus *Eupsophus* is characterized by endotrophic larvae that inhabit water-filled cavities. The larvae feed from large yolk reserves during metamorphosis. The external morphology has been described for four of the ten known species and data on larval chondrocranial morphology are available only for one. We describe the external morphology, oral disc and chondrocranial anatomy of the larvae of *Eupsophus queulensis*. The characteristics of *E. queulensis* tadpoles are compared with those of other *Eupsophus* larvae.

Introduction

The genus *Eupsophus* consists of 10 recognized species, including the recently described *Eupsophus queulensis* (Veloso et al., 2005). They are distributed throughout the temperate forests of southern Chile and Argentina. The larvae of only four species of *Eupsophus* have been described so far: *E. roseus* (Formas & Pugín, 1978), *E. emilopugini* (Formas, 1989*a*), *E. calcaratus* (Formas, 1989*b*; Vera Candioti et al., 2005) and *E. vertebralis* (Formas, 1992). These larvae have been classified as endotrophic-nidicolous (Altig & Johnston, 1989). They are characterized by having few denticles, scarce pigmentation, and internal organs visible through the unpigmented ventral skin.

Herein, we describe and illustrate the external morphology of the tadpole of *Eupsophus queulensis* and its chondrocranial anatomy, comparing the characteristics of this species with those previously described for the genus.

Materials and method

Alberto Veloso and Klaus Busse collected a clutch of eggs, along with a guarding adult female, from a water-filled cavity at the type locality, Reserva Nacional Los Queules (35°59'S,

Source : MNHN, Paris

72°41'W), Maule Region, Chile, on November 2003. The female was included among the type series in the description of the species (VELOSO et al., 2005). The eggs were brought and hatched in the laboratory. Four larvae developed and they were used in this description. Specimens were fixed in 95 % ethanol and subsequently preserved in 10 % commercial grade formalin. Tadpoles are in Gosner stage 34 (GOSNER, 1960).

Measurements, terminology and labial tooth row formula follow ALTIG & MCDIARMID (1999). Measurements were taken using an eye micrometer under a Wild M3C Leica stereomicroscope. The description of larval external morphology is based on the examination of four larvae (Cárdenas-Rojas Field Number DRCR 062). After examination of external morphology, two larvae were prepared for scanning electron analysis. The other two larvae were deposited at the herpetological collection of the Instituto de Zoología Universidad Austral de Chile (IZUA), Valdivia, Chile. Tadpole illustration is based on individual IZUA 3708. The other specimen was used for analysis and description of chondrocranial anatomy (IZUA 3709); the specimen was cleared and double-stained for bone and cartilage using a modified technique of DINGERKUS & UHLER (1977). Chondrocranial terminology follows HAAS (1995, 2003) and LARSON & DE SÁ (1998). Illustrations of larval morphology and chondrocranial anatomy were made using a Wild M3C Leica stereomicroscope with a camera lucida attachment.

RESULTS

DESCRIPTION OF TADPOLE

Tadpoles of *Eupsophus queulensis* have an elliptical body (fig. 1). The snout is rounded in dorsal and lateral views, the dorsal contour of the body gradually curved from mid-body to snout. The nostrils are situated midway between the tip of snout and the anterior border of eyes. The eyes are large, they are laterally positioned and directed anterodorsally, they are separated by a distance 1.9 × the eye diameter. The spiracular tube is absent, the spiracular opening is small, lateral and sinistral. The length of the tail is nearly twice the body length, the dorsal and ventral fins are well developed and almost parallel to the tail musculature, the dorsal fin originates on the posterior third of the body and the ventral fin originates posterior to the vent tube. The caudal musculature is moderately robust with poorly defined myotomes; the tail tip is rounded. The vent tube and opening are medial. The color of preserved specimens is yellowish white whereas the abdomen and fins are transparent and the internal organs are visible. The dorsal surface area is light brownish with scarce and minute melanophores.

The oral disc is positioned ventrally, it is not emarginated and it possesses a single row of marginal papillae with a wide rostral gap (about 1/3 of the anterior labium), submarginal papillae are absent (fig. 2). The labial tooth row formula is 2(2)/2, the posterior labial tooth rows are about equal in length. The upper and lower jaw sheaths are pigmented for about one-third of their width and have serrated edges.

Source : MNHN, Paris

Fig. 1 – Lateral view of *Eupsophus queulensis*, IZUA 3708, Gosner stage 34 tadpole. Bar: 5.0 mm

Fig. 2 – Oral disc of *Eupsophus queulensis*, IZUA 3708, Gosner stage 34 tadpole. Bar: 0.5 mm

Source : MNHN, Paris

Fig. 3 – Suprarostral cartilages of *Eupsophus queulensis*, IZUA 3709, Gosner stage 34 tadpole. Bar 0.5 mm

Measurements in millimeters of tadpole IZUA 3708, following ALTIG & MCDIARMID's (1999) methodology, are as follows. body length 6.3; body height 3.7, body width 4.2, tail length 12.0; maximum tail height 4.5; tail muscle height 2.2; tail muscle width 1.9; interorbital distance 2.9; internarial distance 1.6, oral disc length 1.9.

CHONDROCRANIUM

The paired suprarostral cartilages support the upper horny beak. Each suprarostral consists of a central body and a lateral wing. The bodies of the suprarostrals are vertically rectangular and they are largely fused to the wings (fig. 3). The bodies of the suprarostrals are connected ventromedially via a narrow cartilage. The lateral wings of the suprarostrals are triangular-shaped; the width of each suprarostral's wing is about twice that of the body, the wings have a short but clearly visible *processus (p.) posterior dorsalis*. The suprarostral bodies and the medial margins of the suprarostrals' wings articulate with the tip of the trabecular horns.

The *cornua trabeculae* are short, less than 20 % of the total chondrocranial length. They project anteriorly from the *planum trabeculare anticum*, diverging from each other and forming a wide and shallow "U". The *cornua trabeculae* are almost uniform in width throughout their length and they curve strongly ventrally to articulate with the suprarostrals (fig. 4A, C). The *p. lateralis trabeculae* is poorly developed and almost indistinguishable; it connects laterally the *cornua trabeculae* with the *p. quadratoethmoidalis* via the *ligamentum quadratoethmoidale*. The posterior confluence of the *cornua trabeculae* is continuous with the *planum trabeculare anticum* and the developing *planum ethmoidale*, the later begins to form the anterior wall of the braincase at this stage. The *tectum nasi* has not yet begun to develop.

At stage 34, the cranial floor is not yet fully chondrified, a thin cartilage closes the *fenestra basicranialis*. Two sets of openings are found on the cranial floor. The anterior pair, the *foramina craniopalatina*, is small and almost not visible, whereas the posterior pair, the *foramina carotica primaria*, is well defined (fig. 4B).

The *cartilago orbitalis* forms the lateral walls of the braincase. However, these cartilages do not connect to the otic capsule yet, consequently, the dorsal and anterior margins of the

Source : MNHN, Paris

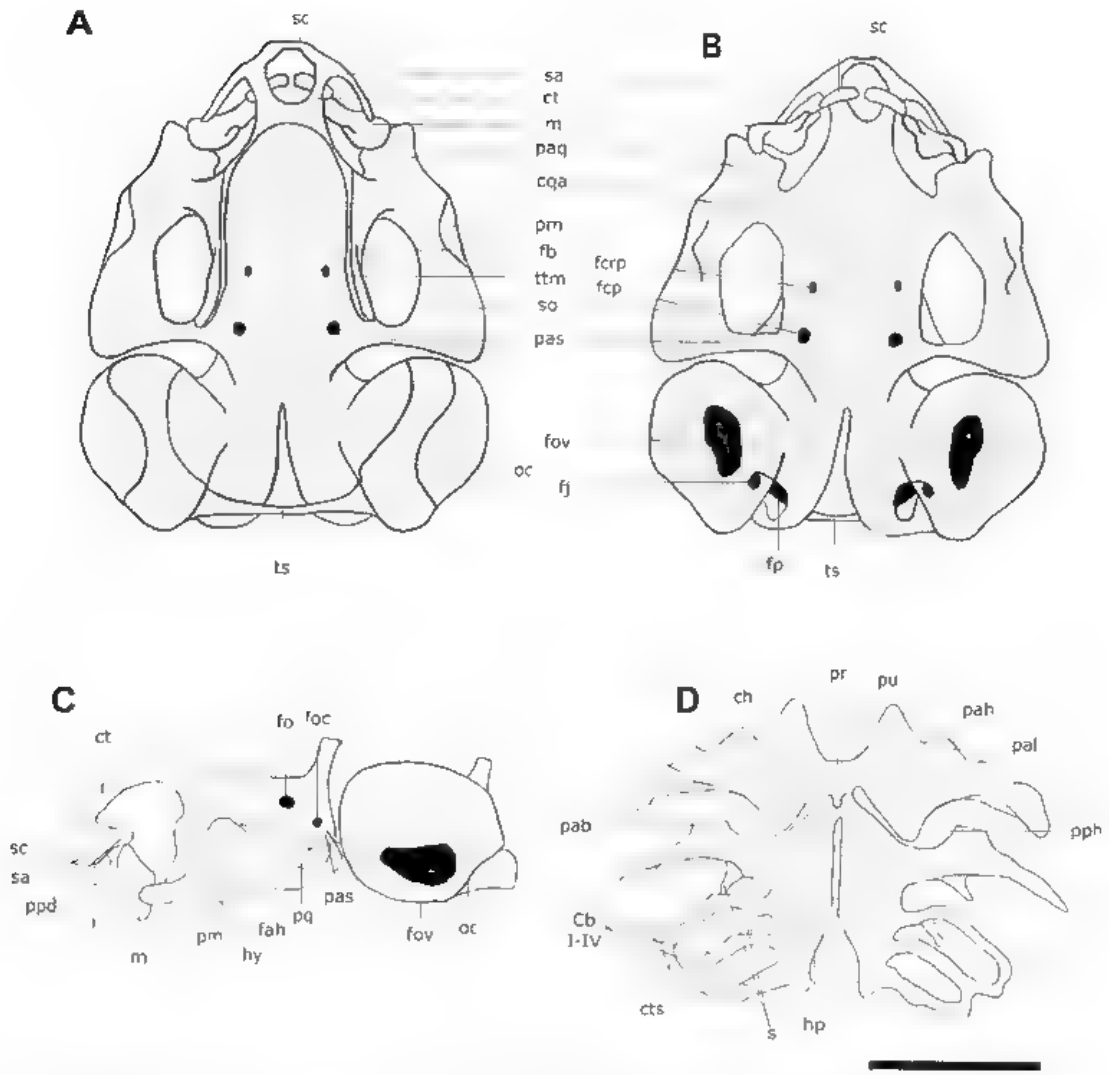

Fig. 4 – Chondrocranium and hyobranchial apparatus of *Eupsophus queulensis*, IZUA 3709, Gosner stage 34 tadpole. (A) dorsal, (B) ventral, and (C) lateral views, (D) ventral view of hyobranchial apparatus. Bar = 1.0 mm. Cb I-IV, ceratobranchial cartilages I-IV, ch, ceratohyal, cqa, *commissura quadratocranialis anterior*, ct, *cornua trabeculae*, cts, *commissurae terminales*, fah, *facies articularis hyalis*, fb, *fenestra basicranialis*, fcp, *foramen caroticum primarium*, fj, *foramen jugulare*, fo, *foramen opticum*, foc, *foramen oculomotorium*, fov, *fenestra ovalis*, fpi, *foramen perilymphaticum inferior*, hp, hypobranchial plate, hy, hyoquadrate process, i, infrarostral cartilage, m, Meckel's cartilage, oc, otic capsule, pa, *processus ascendens*, pab, *processus anterior branchialis*, pah, *processus anterior hyalis*, pal, *processus anterolateralis hyalis*, paq, *pars articularis quadrati*, pm, *processus muscularis*, ppd, *processus posterior dorsalis*, pph, *processus posterior hyalis*, pr, *pars reunens*, pu, *processus uropbranchialis*, sa, suprarostral *ala*, sc, suprarostral *corpus*, s, *spicula*, so, suborbital bar of palato quadrate, ts, *tectum synoticum*, ttm, *taenia tecti marginalis*

Source : MNHN, Paris

foramen (f.) prooticum are open (fig. 4C). The *f. opticum* and the *f. oculomotorium* perforate the *cartilago orbitalis*, the later being the smaller of the two and found posterior and ventrally to the former.

The *fenestra frontoparietalis* is not yet complete. Laterally, we found very thin *taeniae tecti marginales*, and posteriorly the *tectum synoticum* is found as a narrow cartilage connecting the otic capsules (fig. 4A).

The otic capsulae are about 33 % of the total chondrocranial length and 38 % of the total chondrocranial width. The ventrolateral surface of the otic capsules bears a large *fenestra ovalis*. A larval *crista parotica* and *p. oticum* are absent. The *arcus occipitalis* extends ventrally from the posteromedial margin of the otic capsule, fusing with the *planum basale* and giving rise to the occipital condyles. The *f. perilymphaticum inferior* is found lateral to the *f. jugulare* on the ventromedial margin of the otic capsule (fig. 4B).

The *cartilago palatoquadrati* has a constant width throughout its length. It has two attachments to the braincase, anteriorly the *commissura quadratocranialis anterior* and posteriorly the *p. ascendens*. The *commissura quadratocranialis anterior* extends between the *cartilago palatoquadrati*, at a level just posterior to the *pars articularis quadrati*, and the floor of the neurocranium (fig. 4A-B). The anterior margin of the *commissura quadratocranialis anterior* bears a triangular *p. quadratoethmoidalis*, which serves as the point of attachment for the *ligamentum quadratoethmoidale*. A very short, almost indistinct, and blunt *p. antorbitalis* is present. The posterior curvature of the *cartilago palatoquadrati* extends slightly beyond the level of attachment of the *p. ascendens* to the braincase. The lateral and posterior margins of the palatoquadrate curve slightly dorsally, giving the palatoquadrate a concave appearance in dorsal view. The *p. ascendens* is a narrow and rod-like cartilage connecting the posteromedial margin of the *cartilago palatoquadrati* to the *cartilago orbitalis*. The *p. ascendens* attaches just posterior to the *oculomotor foramen*, i.e., SOKOL's (1981) intermediate condition. The *p. ascendens* is almost perpendicular (85-90 angle) to the main axis of the chondrocranium (fig. 4A-C).

Anteriorly, the *cartilago palatoquadrati* has two processes, the *p. muscularis quadrati* and the *pars articularis quadrati*. The *p. muscularis* is broad, flat, and extends dorsally from the lateral margin of the *cartilago palatoquadrati* posterior to the *pars articularis quadrati*. The *p. muscularis* is visible in lateral view. The dorsal edge of the *p. muscularis* inclines medially; a *commissura quadratoorbitalis* is absent. Immediately below the *p. muscularis* and ventrally on the *cartilago palatoquadrati* there is a notch, the *facies articularis hyalis*, which serves as the point of articulation of the ceratohyal with the *cartilago palatoquadrati*. On the articular surface is the hyoquadrate process which in lateral view is a small and sub-triangular process. The *pars articularis quadrati* is slightly angled medially and articulates broadly with the *cartilago Meckeli*.

Meckel's cartilages, together with the infrarostral cartilages, form the mandible during larval stages. Meckel's cartilage is stout and has a sigmoid-shape; its anteromedial margin is concave whereas its anterolateral margin is convex. Laterally, the *cartilago Meckeli* articulates with the *pars articularis quadrati* via the *p. retroarticularis*. This process curves ventrally beneath the *pars articularis quadrati*. Anteromedially, the *cartilago Meckeli* has two processes, the *p. dorsomedialis* and the *p. ventromedialis*. The posterodorsal portion of the infrarostrals cartilages articulates with Meckel's cartilages between these two processes. The infrarostral

Source : MNHN, Paris

cartilages provide support for the lower keratinized beak. Each infrarostral is rectangular in shape and outwardly rounded over their entire anterior margin

HYOBRANCHIAL APPARATUS

The *ceratohyalia* are medially wide and flat cartilages; laterally, they are twisted dorsally to articulate with the *cartilago palatoquadrati* at the *facies articularis hyalis* Each ceratohyal bears two processes on the anterior margin, a triangular *p. anterior hyalis* and a rounded and small *p. anterolateralis hyalis* The *ceratohyalia* also have a well-developed *p. posterior hyalis*. Medially, the *ceratohyalia* are connected by a *pars reunens*, which is continuous with the *copula posterior*. Posteroventrally, the *copula posterior* has a small *p. urobranchialis* The *copula posterior* is continuous with the hypobranchial plates. The hypobranchial plates do not contact each other medially; they are continuous with the ceratobranchials (Cb). Posteriorly, the hypobranchial plates diverge and their posterior edges form an inverted V (fig 4D)

The branchial baskets consist of four ceratobranchials (Cb I-Cb IV). The *p. branchialis* is absent. The ceratobranchials are distally continuous via the *commissurae terminales*, except between Cb I and Cb II. Proximally, ceratobranchial I is attached to the hypobranchial plate by a wide strip of cartilage, Cb I bears a wide and flattened *p. anterior branchialis* on its anterior margin. Ceratobranchials II, III and IV are fused to the hypobranchial plate, the former two via a narrow bar of cartilage and Cb IV via a wider cartilaginous connection Only ceratobranchial I and II bear poorly developed *spiculae*, near their point of attachment to the hypobranchial plate.

DISCUSSION

The tadpoles of *Eupsophus queulensis* are very similar in morphology and color patterns to those of *E. roseus*, *E. emilropugini*, *E. calcaratus* and *E. vertebralis* (FORMAS & PUGÍN, 1978, FORMAS, 1989*a*-*b*, 1992; VERA CANDIOTI et al., 2005). They have elliptical body, approximately two times longer than higher, their tail length is almost twice the body length Eyes are positioned dorsolaterally. The creamy white color and scant pigmentation are common traits of endotroph nidicolous tadpoles (THIBAUDEAU & ALTIG, 1999).

Eupsophus tadpoles differ in a few characteristics The spiracular tubes of *Eupsophus emilropugini* and *E. vertebralis* are short, sinistral and ventrolaterally located (FORMAS, 1989*a*, 1992) *Eupsophus queulensis*, *E. roseus* (FORMAS & PUGÍN, 1978) and *E. calcaratus* (FORMAS, 1989*b*) share a small and sinistral spiracular opening without spiracular tube. A single, sinistral, and ventral spiracular tube with a visible opening has been previously reported for *E. calcaratus* (VERA CANDIOTI et al., 2005). Tadpoles of *E. calcaratus* (IZUA 2896-2897, 2957) examined herein do not have spiracular tube. The lack of a spiracular tube is a modification for tadpoles with nidicolous life history (THIBAUDEAU & ALTIG, 1999).

The oral disc of *E. queulensis* and all described *Eupsophus* larvae does not differ from that of typical exotrophic larvae It is ventral and has a single row of marginal papillae with a

Source : MNHN, Paris

distinct rostral gap. The reported labial tooth row formulae range from 2/2 in *E. roseus* (FORMAS & PUGÍN, 1978), *E. emiliopugini* (FORMAS, 1989*a*) and *E. calcaratus* (FORMAS, 1989*b*) to 2(2)/2 in *E. queulensis* (this work) and 2(2)/2(1) in *E. vertebralis* (FORMAS, 1992). The presence of a vestigial third posterior row in one individual and the following intraspecific variation was reported for larvae of *E. calcaratus*, 2(2)/2, 2(2)/2(1) (VERA CANDIOTI et al., 2005).

Only the chondrocranium of *Eupsophus calcaratus* had been described so far (VERA CANDIOTI et al., 2005). Herein we compare the main differences between *E. queulensis* (stage 34) and *E. calcaratus* (stage 31); characteristics for *E. calcaratus* are given in parenthesis. *Eupsophus queulensis* has body and wings of the suprarostrals largely fused (joined by a cartilaginous dorsal bridge), the trabecular horns are of uniform width throughout their length (anteriorly narrow); the trochlear foramen is absent (present); the *p. ascendens* of the palatoquadrate has an intermediate attachment to the braincase (low attachment); the infrarostrals are connected medially through connective tissue (infrarostrals fused into a single element), *commissurae terminales* are absent between Cb I and Cb II (present), and *spiculae* absent in Cb III and Cb IV (present in Cb III).

Based on adult morphology, karyotypes, call characteristics, and a recent molecular phylogeny, the ten species currently included in the genus *Eupsophus* have been separated into two species groups, the *roseus* and the *vertebralis* groups (FORMAS 1980, 1991, 1993; FORMAS et al., 1983, 1992, FERNANDEZ DE LA RIGUERA, 1987, PENNA & VELOSO, 1990; ORTIZ & IBARRA-VIDAL, 1992; PENNA & SOLIS, 1995; NÚÑEZ et al., 1999; NÚÑEZ, 2003). The available chondrocranial data are restricted to two species of the *roseus* group. Given the lack of baseline tadpole data, it is not yet possible to determine if larval characteristics (external and internal) can provide additional support to differentiate the two groups.

RESÚMEN

El género *Eupsophus* se caracteriza por poseer larvas endotróficas que habitan cavidades con agua. Durante la metamorfosis las larvas se sustentan de sus grandes reservas vitelinas. La morfología externa ha sido descripta para cuatro de las diez especies conocidas en el genero; características de la anatomía condrocraneal fueron reportadas sólo para una especie. En este trabajo se describen la morfología larval externa, el disco oral larval y la anatomía condrocraneal de *Eupsophus queulensis*. Las características de la larva de esta especie se comparan con las de otras larvas en el género *Eupsophus*.

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Source : MNHN, Paris

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New synonyms in specific names of frogs (Raninae) from the border regions between China, Laos and Vietnam[1]

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Species pairs described on either side of the Chinese/Vietnamese-Lao border are compared and the following new synonyms are proposed: *Rana daorum* is a subjective junior synonym of *Amolops mengyangensis* and the valid name of the species is *Amolops mengyangensis*; *Rana hmongorum* is a subjective junior synonym of *Rana jingdongensis* and the valid name of the species is *Odorrana jingdongensis*; *Rana megatympanum* and *Rana heatwolei* are subjective junior synonyms of *Rana tiannanensis* and the valid name of the species is *Odorrana tiannanensis*; *Rana nigrolineata* is a subjective junior synonym of *Rana lateralis* and the valid name of the species is *Pelophylax lateralis*; *Rana nigrotympanica* is a subjective junior synonym of *Rana cubitalis* and the valid name of the species is *Sylvirana cubitalis*; *Rana bannanica* is a subjective junior synonym of *Rana milleti* and the valid name of the species is *Sylvirana milleti*. Evidence from morphological and morphometrical study of type material and topotypical material is given. Attention is drawn to the fact that taxonomy is an international endeavour, and that describing new taxa often requires knowing the fauna of neighbouring countries.

INTRODUCTION

Preliminary to any systematic work we need to define the samples we have to study. Some groups may be of small size, so there is no major problem to compare all their members. Others may count numerous species and taxonomic delimitation may be very poor. In some cases also allocation of an observed taxon to a particular group will be difficult, and in the end no relevant comparison will be done.

1. This paper is issued from a communication entitled "Transborder systematics: a critical evaluation of zoogeography and conservation biology at the crossroads between Vietnam, Laos and China", presented during the 13th Ordinary General Meeting of the Societas Europaea Herpetologica (SEH) in Bonn (Germany) on 30 September 2005.

Source : MNHN, Paris

Another fact is that in recent years many new species have been described and the discovery of many more is expected (Kohler et al., 2005), which suggests to the taxonomist that what he has in his hands could be probably new. And it can, but sometimes it won't. Thirty percent of the amphibian species are poorly known, only the original description and a few old records are available and no proper figure or photograph have been published.

Many authors focus on the southern limit of Oriental region, known as the Wallace line (Oosterzee, 1997), but the north-eastern limit of this region is still more problematic and quite unique among realms. Over a distance of several thousands kilometers, no geographic limits, such as deserts or high mountains, exist between the Palearctic realm and the Oriental realm, so that an intergradation zone of roughly 1500 km has developed. In fact in a large zone, including central and southern China, northern Vietnam and small parts of northern Laos, north-eastern India, northern Thailand and northern Myanmar, members of the two faunas co-exist in the same habitats (*Hyla* sensu stricto, *Rana* sensu stricto are found along with *Xenophrys*, *Odorrana*, etc.), and members of both faunas might have their major centre of diversification in this region (e.g., in *Hyla* and *Xenophrys*).

The border between China on one hand, and Laos and Vietnam on the other, has been used as a limit for biogeographical investigations (Inger, 1999; Zhao, 1999), although it does not correspond to any natural limit. In many studies by Chinese authors, insufficient comparison with the Indochinese species has been done due to work in isolated conditions, so that synonyms have been created, some of which still need to be clarified. In recent times, taxonomic works have been carried out in Vietnam without comparison to the Chinese fauna (Bain et al., 2003), thus again creating new names for already named species.

Another problem of the work of Bain et al. (2003) is that, although they provided comparisons to many of the "stream frogs" from the Oriental region, they did not refer to the voucher specimens they studied, nor gave the geographical origin of these specimens. In consequence, verification of specific allocation of these species cannot be carried out and distinctive characters might be useless or uninformative in some cases (see below for *Rana limongorum*). Use of such specimens for further analyses, such as phylogenetic hypotheses and classificatory proposals based on them (Frost et al., 2006), introduces important doubts about the results obtained.

The aim of this study is to confront information in some pairs of nominal species of the Oriental region in order to understand taxonomic allocation of specimens to biological species and to have additional data on their distribution. In many cases this provides more data on biology and conservation of the species, as often one of the two species is better known. In this first clarification (to be followed by others), pairs of names available for six ranine frogs of the genera *Amolops*, *Odorrana*, *Pelophylax* and *Sylvirana* will be discussed.

Material and methods

Material

See appendix 1.

Source : MNHN, Paris

CLASSIFICATION

FROST et al. (2006) published an important and necessary work in presenting a tree of all amphibians. Nevertheless the sampling is not equally distributed and the Oriental ranid frogs are particularly poorly represented as compared to the diversity of lineages. In conclusion, FROST et al. (2006) decided to lump large groups of frogs (e.g., *Huia* Yang, 1991) but kept other lineages apart without any evidence beside original definition (e.g., *Pterorana* Kiyasetuo & Khare, 1986). For this reason, I here still keep the groups proposed as subgenera by DUBOIS (1992), but use them as genera. *Odorrana* Fei, Ye & Huang, 1990 (type species by original designation *Rana margaretae* Liu, 1950) is applied here to a group of frogs with its centre in China and northern Vietnam and northern Laos. These frogs are stream-living species with long legs, but shorter than in *Amolops* Cope, 1865. In particular they can be distinguished by the shape of their toe pad grooves which always show a little terminal gap in *Odorrana* (OHLER & DUBOIS, 1989). Their tadpoles have neither abdominal suckers nor glands on head and back; they show 4 rows of keratodonts on lower lip. *Huia* as defined by YANG (1991*a*) is a group of frogs with tadpoles bearing abdominal suckers and with adults having longer legs than those of *Amolops*. It was originally erected for species from Borneo, Java, Thailand and Yunnan. YANG (1991*b*) added *Rana nasica* Boulenger, 1903 to this genus on the basis of tadpoles allocated to this species, but identity of these tadpoles was supported by morphological evidence only. Thus the taxonomic allocation of this species must be studied again on properly identified specimens and *Rana nasica* cannot be used as voucher for *Huia* as done in FROST et al. (2006). Allocation of recently described frogs to *Huia* must be re-evaluated in further works as it was done on adult morphology only, and as taxonomic conclusions were not based on type species but on species that might be phylogenetically closer to other clades than to that containing *Rana cavitympanum* Boulenger, 1893 (type species of *Huia* Yang, 1991 by original designation).

METHODS

For most of the name-bearing types of the Oriental region, detailed description and photographs of the specimens are available at MNHN. These descriptions will be published elsewhere, in particular in a revision of *Silvirana* (OHLER & DUBOIS, in preparation). For recent names, good original descriptions are available. Morphological comparison of type material, topotypical material and specimens from various localities in the Oriental region was carried out based on voucher specimens or descriptions. Morphometric measurements of basic characters such as snout-vent length (SVL), head width (HW), head length (HL), tibia length (TL) and tympanum diameter (TYD) were made if necessary and are compared with published measurements. The following terms are used in the synonymies below (DUBOIS, 2006): *hypodigm* (SIMPSON, 1940) for a set of specimens used by an author to establish and describe a new species, *onomatophore* (SIMPSON, 1940) for the name-bearing type of a taxon, *onymotope* (DUBOIS, 2005*a-b*) for the type locality of a species.

Contrary to the methods available to point to differences, there is no methodology for the definition of synonyms. A synonym clearly cannot be defined as "identical", as within a biological species different kinds of morphological variation (sexual dimorphism,

Source : MNHN, Paris

ontogenetical variation, life stages) occur, caused either by genetic of by epigenetic factors, or both To establish synonymy, we need information on the intraspecific variation in order to show that the synonymous taxon falls within the range defined for the other taxon But often the data available on various species are very poor (about 30 % of "data deficient" species in the Global Amphibian Assessment, STUART et al., 2004). Also as in an example below, males of one taxon and females of another taxon might be available and thus no direct comparison possible. In such a case, sexual dimorphism must be evaluated by comparison with phylogenetically close taxa

A very particular problem in anurans is intraspecific variation in size. DUBOIS (1976) proposed a *ratio of extreme values* (RE) which divides the size of the largest known specimen of a species by the smallest known of this species. If applied to species recognized on biological criteria as the treefrogs of the genus *Hyperolius* Rapp, 1842 described by SCHIOTZ (1999), RE of adult male frogs varies from 1 04 to 1 56. In *Afrixalus* Laurent, 1944 the value of RE is between 1 11 and 1 42 A value of 1 5 means that the smallest male has a SVL of two thirds of that of the largest known male. The sole presence of size variation cannot be used as a taxonomic argument. It may be due to variation in presence of age classes in a particular population or to variation in external factors such as predation or harvesting On the other hand, size, independent of its origin, is linked to allometric variation in different body parts such as tibia length, head shape, etc , and might lead to differences in relative size of various body parts. If the sample is large enough, detailed analysis on growth can be made especially using comparison of slopes of allometric growth curves. But on small samples, which are often the samples we have to deal with in taxonomy, systematic studies can have only poor arguments. Nowadays, size variation alone is not considered a sufficient argument for defining a species. Like any other character, only its correlation to other characters will be considered as sufficient support to indicate genetic isolation of a group of frog to others such groups, and its meaning will be different in situations of sympatry, parapatry or allopatry.

ABBREVIATIONS

Collections

BMNH The Natural History Museum, London, United Kingdom
CIB – Chengdu Institute of Biology, Chengdu, China.
FMNH – Field Museum of Natural History, Chicago, USA
KIZ. – Kunming Institute of Zoology, Kunming, China
MAS – Malcolm A. Smith collection
MNHN. – Muséum national d'Histoire naturelle, Paris, France
MSNG. – Museo di Storia Naturale di Genova, Genova, Italy
ROM. – Royal Ontario Museum, Toronto, Canada
ZSI – Zoological Survey of India, Kolkota, India

Abbreviations used in text and tables

♂ – Adult male
♀ – Adult female
alt – Altitude above sea level (in metres)
n. – Sample size

Source : MNHN, Paris

HL. – Head length
HW. – Head width
SVL. – Snout-vent length.
TL. – Tibia length.
TYD. – Tympanum diameter

TAXONOMIC DISCUSSIONS

Amolops mengyangensis Wu & Tian, 1995

Amolops mengyangensis Wu & Tian, 1995 50 HYPODIGM: 3 ♂ – ONOMATOPHORE Holotype, by original designation, CIB 579034, ♂, SVL 38 7 mm (personal observation) – ONYMOTOPE Mengyang (22°04'N, 100°53'E; alt 680 m), Xishuanbanna Daizu Zizhizhou, Yunnan Sheng, China.

Rana daorum Bain, Lathrop, Murphy, Orlov & Ho, 2003. 38 HYPODIGM 48 ♂, 10 ♀, 1 subadult ♀ ONOMATOPHORE Holotype, by original designation, ROM 26381, ♀, SVL 55 7 mm ONYMOTOPE Approximately 5 km NW of Sa Pa Village, near O Qui Ho Pass (22°20'09''N, 103°50'14''E, alt 1400 m), Lao Cai Province, Vietnam – STATUS: **New synonym.**

Amolops chunganensis (Pope, 1929) was reported to occur in southern Yunnan (Mengyang) by YANG (1991*a*) In 1995, WU & TIAN described a new species, *Amolops mengyangensis*, from specimens previously reported as *Amolops chunganensis* OHLER et al. (2000) reported the presence of *Amolops chunganensis* in northern Vietnam. These specimens (MNHN 1999 5799-5813) are the same biological species as those described as *Rana daorum* by BAIN et al. (2003). Comparison of the hypodigm of *Amolops mengyangensis* (fig. 1a) with topotypes of *Rana daorum* (fig. 2a), as well as re-evaluation of the characters indicated by BAIN et al. (2003), in particular absence of vomerine teeth, small tympanum/eye ratio and morphometric data (tab. 1), support the synonymy of the two nominal species.

These frogs can be assumed to be a different taxon from *chunganensis* as proposed by WU & TIAN (1995) and BAIN et al (2003), but should be placed in the genus *Amolops*, because of the presence of a continuous fold on the ventrolateral border of their toe pads and their long legs, similar to the species *Amolops monticola* (Anderson, 1871) and *Amolops chunganensis* These species of *Amolops* have dorsolateral folds, white upper lip and toe pads that are rounded but not transversally enlarged as in *Amolops formosus* (Günther, 1876) or allied species, nor pointed as in *Odorrana* (OHLER & DUBOIS, 1989).

Amolops chunganensis was described from Fujian and has been reported from southeastern and western China (FEI, 1999) It should be removed from the species lists of amphibians of Vietnam and Yunnan as the vouchers are specifically identical with *Amolops mengyangensis*.

Source : MNHN, Paris

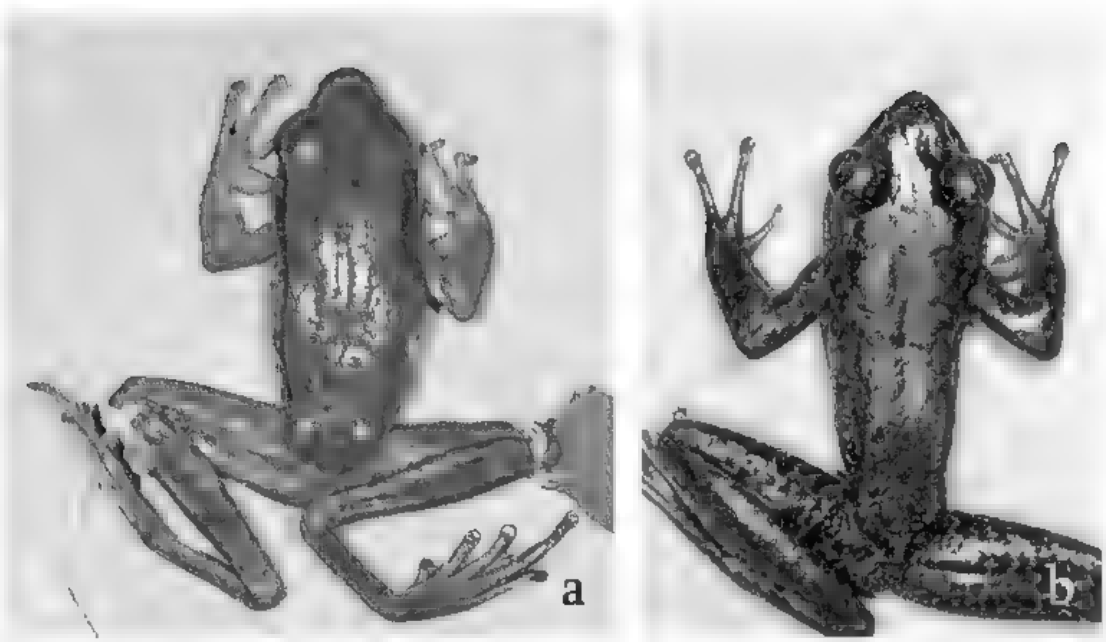


Fig. 1 – (a) *Amolops mengyangensis* Wu & Tian, 1995 Holotype, CIB 579034, ♂, SVL 38.4 mm, Mengyang, Yunnan, China, in dorsal view (b) *Odorrana jingdongensis* Fei, Ye & Li, 2001 Topotype of *Rana hmongorum* Bain, Lathrop, Murphy, Orlov & Ho, 2003, MNHN 1999.5772, ♂, SVL 64.0 mm; Sa Pa, Vietnam, specimen in life in dorsal view

Table 1 Measurements of *Amolops mengyangensis* Wu & Tian, 1995, including type specimens of *Amolops mengyangensis* Wu & Tian, 1995, type specimens and topotypes of *Rana daorum* Bain, Lathrop, Murphy, Orlov & Ho, 2003 Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the type specimens of *Rana daorum* which are from Bain et al. (2003), note that their measurements of head length (in italics) have been taken on radiographs and cannot be compared to standard measures.

Measurement	*Amolops mengyangensis* Yunnan		*Rana daorum* Vietnam			
	Holotype	Paratypes	Holotype	Paratypes	Paratypes	Topotypes
	n = 1	*n* = 2	*n* = 1	*n* = 7	*n* = 8	*n* = 17
SVL	38.7	38.3-38.5	55.7	34.8-38.1	53.3-57.6	36.4-4[illegible]
HW	12.3	12.3-12.7	18.8	11.1-13.0	15.6-17.6	11.4-12.[illegible]
HL	14.4	13.4-14.2	*25.4*	*16.5-21.0*	*16.7-19.4*	12.7-14.4
TL	23.1	21.5-23.7	33.6	19.1-23.5	32.7-36.4	20.7-25.1

Source : MNHN, Paris

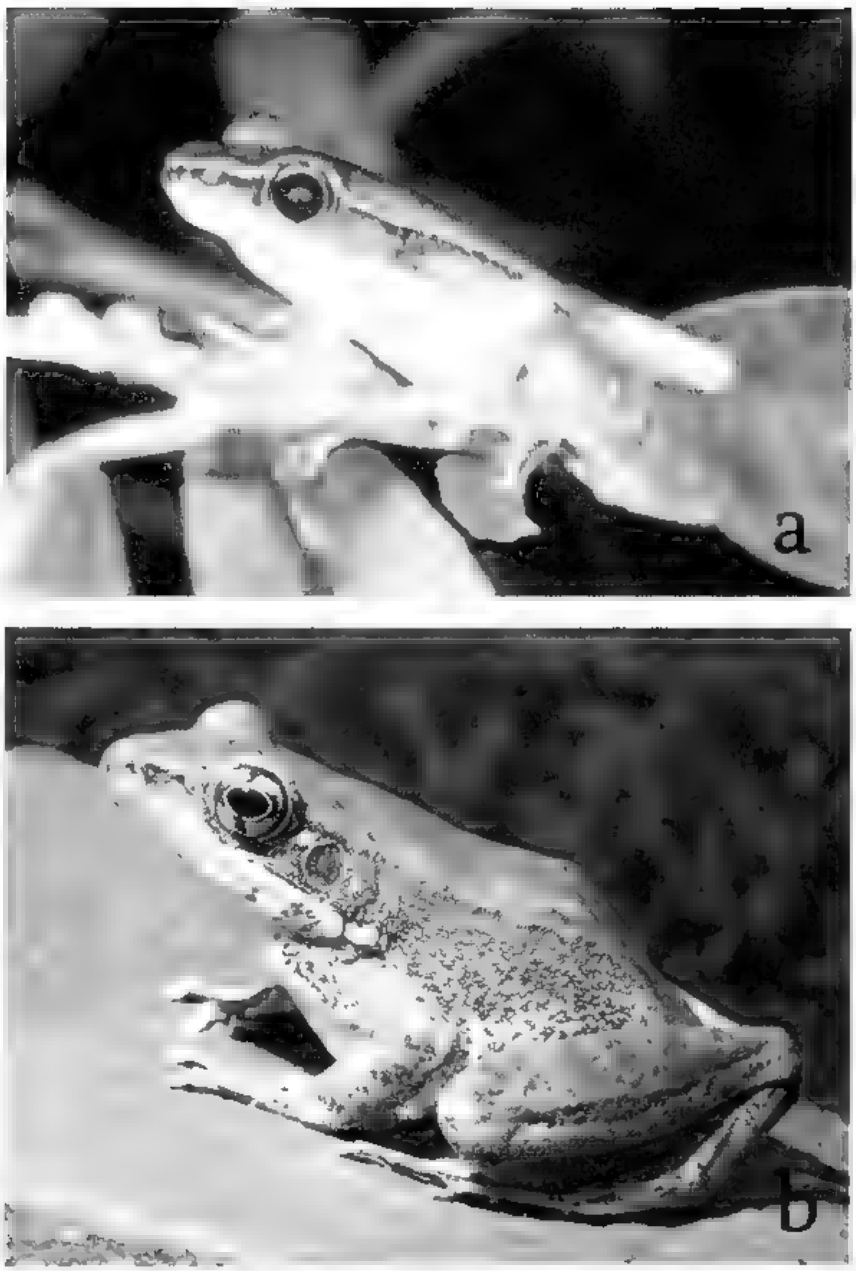


Fig. 2. (a) *Amolops mengyangensis* Wu & Tian, 1995. Topotype of *Rana daoxiangensis* Bain, Lathrop, Murphy, Orlov & Ho, 2003, MNHN 1999.5813, ♂, SVL 37.5 mm, Sa Pa, Vietnam, specimen in life at night. (b) *Odorrana tiannanensis* Yang & Li, 1980, MNHN 2004.0408, ♀, SVL 104.1 mm; Nathen, Phongsaly Province, Laos, specimen in life.

Source : MNHN, Paris

Odorrana jingdongensis Fei, Ye & Li, 2001

Odorrana jingdongensis Fei, Ye & Li, 2001: 110 – HYPODIGM 3 ♂, 11 ♀, tadpoles ONOMATOPHORE Holotype, by original description, CIB 581505, ♀, SVL 90 4 mm ONYMOTOPE Xinminxiang (24°45'N, 100°75'E; alt. 1480 m), Jingdong Xian, Yunnan Sheng, China.
Rana hmongorum Bain, Lathrop, Murphy, Orlov & Ho, 2003. 40 – HYPODIGM: 15 ♂, 24 ♀, 5 young ONOMATOPHORE Holotype, by original designation, ROM 26376, ♀, SVL 86 8 mm ONYMOTOPE Approximately 5 km NW of Sa Pa Village, near O Qui Ho Pass (22°20'09''N, 103°50'14''E, alt. 1400 m), Lao Cai Province, Vietnam. – STATUS: **New synonym**

Until 2001, the name *Odorrana andersonii* was used for a group of sibling species of frogs occurring over a large range in southern China and the northern Oriental region *Rana andersonii* Boulenger, 1882 had been first described as *Polypedates yunnanensis* Anderson, 1879 from Hotha valley in Yunnan. As this name was then a secondary homonym in the genus *Rana* Linnaeus, 1758, BOULENGER (1882) coined a replacement name. The only extant syntype (BMNH 1947 2 2 60) is a subadult male of 50.0 mm in SVL. FEI et al (2001) revised the frogs of the *andersonii* group and described two new species from China, thus limiting *Odorrana andersonii* to north-western Yunnan (Longling and Tengchong Counties)

Without reference to the works of the Chinese authors and without comparison with the syntypes of *Polypedates yunnanensis*, BAIN et al (2003) described *Rana hmongorum* from Sa Pa based on specimens similar to those called *Rana andersonii* by BOURRET (1942) and OHLER et al (2000) (fig. 1b). BAIN et al. (2003) gave differences to specimens allocated to *Rana andersonii* but without indicating origin of these specimens or collection references. As they did study neither type specimens nor topotypical specimens of the existing or newly coined species group names, their conclusions are not convincing, and as we do not have any information on the voucher specimens referred by them to *Rana andersonii*, their comparisons are useless as several new taxa have been recognized in this group recently Comparisons are here provided for morphometric data (tab 2) concerning the purported diagnostic characters of *Odorrana jingdongensis* and *Rana hmongorum*. In these species, the discs of fingers are moderately expanded, indicated as 1 4 times the width of third fingers in the description of *Odorrana jingdongensis*, and as less than twice the base of phalanges in the description of *Rana hmongorum*. All fingers have lateroventral grooves joining terminally very closely in *Rana hmongorum* For both species terminal phalanges are described as T-shaped The animal pole of eggs is described as unpigmented in *Odorrana jingdongensis* and as white in *Rana hmongorum* Geographical distribution is continuous as the onymotopes of *Odorrana jingdongensis* and *Rana hmongorum* are in the same mountain range. On the basis of morphological character study, *Rana hmongorum* should be considered a junior subjective synonym of *Odorrana jingdongensis*, with the valid name *Odorrana jingdongensis*

Odorrana tiannanensis (Yang & Li, 1980)

Rana tiannanensis Yang & Li, 1980 261 HYPODIGM 2 ♂, 4 ♀. – ONOMATOPHORE: Holotype, by original designation, KIZ 77.1 0185 ♂ 52 5 mm. – ONYMOTOPE. Dawei Shan (alt 1200 m), Hekou Xian (22°31'N, 103°59 E), Yunnan Sheng, China

Source : MNHN, Paris

Table 2 Measurements of *Odorrana jingdongensis* Fei, Ye & Li, 2001, including type specimens of *Odorrana jingdongensis* Fei, Ye & Li, 2001, type specimens and topotypes of *Rana hmongorum* Bain, Lathrop, Murphy, Orlov & Ho, 2003. Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the type specimens of *Odorrana jingdongensis* which are from FEI, YE & LI (2001) and those of the type specimens of *Rana hmongorum* which are from BAIN et al. (2003); note that measurements of head length by the latter (in italics) have been taken on radiographs and cannot be compared to standard measures. The maximum value for TL in ♂ paratypes of *Rana hmongorum* given as 51.2 mm (in bold) is probably in fact close to 41.2 mm.

Measurement	*Odorrana jingdongensis* Yunnan		*Rana hmongorum* Vietnam			
	Paratypes ♂ *n* = 5	Holotype and paratypes ♀ *n* = 19	Topotypes ♂ *n* = 8	Topotypes ♀ *n* = 2	Paratypes ♂ *n* = 12	Holotype and paratypes ♀ *n* = 10
SVL	62.0-81.5	64.7-108.0	52.9-64.0	75.0-77.7	54.7-65.3	74.3-86.8
HW	20.5-26.6	20.6-36.4	19.5-22.3	27.3-27.6	18.9-21.1	29.2-31.3
HL	21.3-29.4	23.5-38.4	21.1-23.3	28.7-29.6	*20.7-30.4*	*37.0-42.3*
TL	37.7-47.7	39.3-61.9	35.5-39.7	45.7-47.7	33.4-**51.2**	43.1-49.2

Rana megatympanum Bain, Lathrop, Murphy, Orlov & Ho, 2003: 50. – HYPODIGM: 4 ♂, 11 ♀. – ONOMATOPHORE: Holotype, by original designation, ROM 39684, ♀, SVL 93.6 mm. – ONYMOTOPE: Khe Moi River (18°56'30"N, 104°48'35"E), approximately 24 km west of Con Cuong village (by road), Con Cuong District, Nghe An Province, Vietnam. – STATUS: **New synonym**.

Rana heatwolei Stuart & Bain, 2005: 487. – HYPODIGM: 6 ♂, 5 ♀. – ONOMATOPHORE: Holotype, by original designation, FMNH 258134, ♂, SVL 57.3 mm. – ONYMOTOPE: Tributary of Nam Ou River (22°05'38"N, 102°12'50"E), Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos. – STATUS: **New synonym**.

Rana tiannanensis was described by YANG & LI (1980) from Hekou, southern Yunnan. It is still known only from a few places close to the Lao-Vietnamese border (YANG, 1991*a*, FEI, 1999). In 2003, BAIN et al. described a frog from northern Vietnam, *Rana megatympanum*, that they considered close to *Rana tiannanensis* but being nevertheless a distinct species because of absence of a vertical lip stripe (present in *R. tiannanensis*), absence of dorsolateral folds in males and discs of toes larger than those of fingers. STUART & BAIN (2005) described a species close to *R. megatympanum* from northern Laos, *Rana heatwolei*, which can be distinguished from the Vietnamese form by the presence of spinules on back and venter and the presence of small dark brown spots.

New material available from northern Laos (Phongsaly Province) adjacent to the Chinese locality of *Rana tiannanensis* and study of descriptions in the Chinese literature (FEI, 1999) show that *Rana tiannanensis* (fig. 2b) cannot be distinguished by any of these characters

Source : MNHN, Paris

Table 3. – Measurements of type specimens of *Odorrana tiannanensis* (Yang & Li, 1980) including type specimens of *Rana tiannanensis* Yang & Li, 1980 and of *Rana megatympanum* Bain, Lathrop, Murphy, Orlov & Ho, 2003, and other specimens allocated to this taxon. Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the type specimens of *Rana tiannanensis* which are from Yang & Li (1980), and those of the type specimens of *Rana megatympanum* which are from Bain et al. (2003); note that measurements of head length by the latter (in italics) have been taken on radiographs and cannot be compared to standard measures.

Measurement	*Rana tiannanensis*				*Rana megatympanum*	
	Yunnan		Laos		Vietnam	
	Holotype and paratype ♂ *n* = 2	Paratypes ♀ *n* = 4	♂ *n* = 8	♀ *n* = 1	Paratypes ♂ *n* = 4	Holotype and paratypes ♀ *n* = 10
SVL	52.3-53.5	90.5-107.6	45.9-56.7	100.2	48.6-55.2	93.6-105.3
HW	19.1-19.3	33.0-34.5	16.0-20.2	36.0	18.0-19.1	34.1-35.7
HL	20.5-20.8	36.0-38.6	18.0-22.2	37.7	*24.6-27.1*	*41.3-47.6*
TL	33.6-34.0	63.2-67.5	31.0-35.1	65.7	32.3-33.1	55.8-67.7
TYD	5.1-5.3	5.35-5.8	6.4-7.9	6.0	4.3-5.1	4.6-5.9

from *Rana megatympanum* or *Rana heatwolei*. Differences are due to incomplete descriptions based on specimens of a single sex and reproductive stage. Striped lips are present in females of specimens allocated to *Rana tiannanensis* (Fei, 1999) as they are in specimens allocated to *Rana megatympanum*. The sexual dimorphism in tympanum size can be confirmed for populations allocated to both species (tab. 3). Ranges of adult size of males and females correspond. Comparison to the newly described *Rana heatwolei* Stuart & Bain, 2005 shows that Lao specimens from Nam Ou valley (onymotope of *R. heatwolei*) share distinct small spots with this new taxon but do not have spinules on body. In conclusion and reconsidering character distribution, *Rana megatympanum* and *Rana heatwolei* should be treated as junior subjective synonyms of *Rana tiannanensis*, with the valid name *Odorrana tiannanensis*.

Pelophylax lateralis (Boulenger, 1887)

Rana lateralis Boulenger, 1887: 483. Hypodygm.: 1 ♂. Onomatophori: Holotype, by monotypy, MSNG 29324, ♂, SVL 53 mm. Onymotopi: Kokarit ["Kaw-ka-riet"] (98°14'E, 16°33'N), east of Moulmein, Karen State, Myanmar.

Rana nigrolineata Liu & Hu, 1959: 510, 516. Hypodygm.: 10 ♂, 8 ♀. Onomatophori: Holotype, by original designation as "type", CIB 571085, ♂, SVL 50.5 mm. Onymotopi: Mengyang (21°37'N, 101°22'E, alt. 680 m), Xishuanbanna Dai Zizhizhou, Yunnan Province, China. Status: **New synonym**.

Source : MNHN, Paris

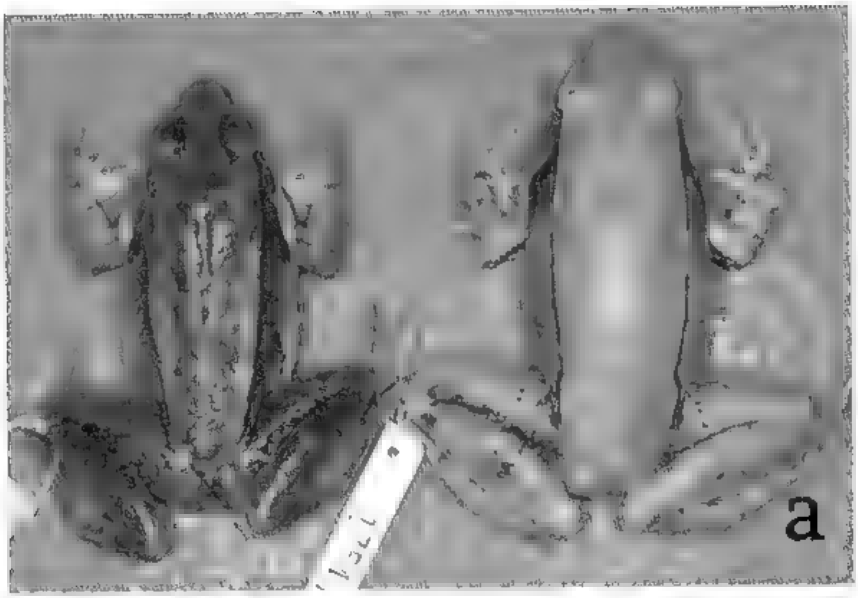
Table 4. Measurements of *Pelophylax lateralis* (Boulenger, 1887), including holotype of *Rana lateralis* Boulenger, 1887, type specimens of *Rana nigrolineata* Liu & Hu, 1959 and other specimens allocated to this taxon. Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the holotype of *Rana lateralis* which are from BOULENGER (1920) and those of the type specimens of *Rana nigrolineata* which are from LIU & HU (1959).

Measurement	*Rana lateralis*			
	Myanmar		Laos	
	Holotype ♂ *n* = 1	♂ *n* = 1	♂ *n* = 9	♀ *n* = 1
SVL	47	51.8	42.5-46.9	48.8
HW	17	17.6	15.7-17.1	16.8
HL	16	18.9	16.4-18.1	17.8
TL	23	24.1	21.7-23.6	~23

Measurement	*Rana lateralis*		*Rana nigrolineata*	
	Thailand		Yunnan	
	♂ *n* = 3	♀ *n* = 3	Holotype and paratypes ♂ *n* = 10	Paratypes ♀ *n* = 8
SVL	52.4-55.0	58.8-67.5	43.0-52.5	51.0-61.3
HW	18.5-22.0	20.9-22.3	14.5-18.4	18.0-21.8
HL	19.2-20.0	21.8-23.0	16.0-20.4	18.9-22.0
TL	23.6-24.7	26.9-31.3	22.5-28.4	26.8-33.0

This frog was originally described from Myanmar. It is currently known to occur in Cambodia, Laos, Thailand and Vietnam. In southern Yunnan, a species of *Pelophylax*, *Rana nigrolineata*, with transversal dorsal stripes, was described by LIU & HU (1959). I had the opportunity to study the holotype of *Rana nigrolineata* and material from near the onymotope of *Rana lateralis* in Myanmar (fig. 3), which prove very similar in general coloration pattern, skin structure and webbing. The holotype of *Rana lateralis* has no oblique dark bands on back according to its original description (BOULENGER, 1887), but oblique granular folds (BOULENGER, 1912). Other specimens from Cambodia (unpublished data), Laos (MNHN 1997.4097-4088), Myanmar (BMNH 1893.10.9.16, MNHN 1893.0456) and Thailand (MNHN field numbers 17543-17544, Y0041-0044) show those stripes more or less distinctly either as granular folds or as dark stripes. In the diagnosis of *Rana nigrolineata*, presence of oblique stripes in all specimens was mentioned (LIU & HU, 1959: 530), as well as external vocal sacs. Vocal sacs of *Rana lateralis* were said to be internal in the holotype, present in specimens from Thailand (TAYLOR, 1962), and appear as external foldings on sides

Source : MNHN, Paris



Source : MNHN, Paris

of the throat in specimens from Laos and Thailand. As internal openings of vocal sacs are present in the holotype, the absence of external sacs may be due to age or reproductive stage of the specimen which is either a subadult or a non-reproductive male. In samples from a single locality, coloration and presence of oblique bands is very variable and cannot be used as a discriminating character. I could measure the holotype of *Rana nigrolineata* and specimens from Laos, Myanmar and Thailand. Comparison of these frogs with those from Yunnan (LIU & HU, 1959) shows minor variation in size (SVL) (♂ RE = 1.29; ♀ RE = 1.39) (tab. 4) and measurements are largely overlapping between all samples. Considering morphological similarity, colour pattern and morphometrics, *Rana nigrolineata* should be considered a junior subjective synonym of *Rana lateralis*.

Sylvirana cubitalis (Smith, 1917)

Rana cubitalis Smith, 1917: 277. – HYPODIGM: 2 ♂. – ONOMATOPHORE: Holotype, by original designation as "type", BMNH 1947.2.2.35 [ex BMNH 1921.4.1.228, ex MAS 1106], ♂, SVL 66.8 mm (given as 68 mm in SMITH, 1917). – ONYMOTOPE: Doi Nga Chang (alt. 490 m [1600 ft.]), [northern Siam, precise locality unknown because name has probably changed], Thailand. – COMMENTS: According to SMITH (1930: 104), the male described and measured by BOULENGER (1920: 138-139) is not the holotype.

Rana (Sylvirana) nigrotympanica Dubois, 1992: 326. – HYPODIGM: 1 ♀, 3 tad. – ONOMATOPHORE: Holotype, by original designation, CIB 571162, ♀, SVL 6[illegible] mm. Description and figures of holotype: LIU & HU, 1959: 518, fig. 4.1-3, 1961: 201, fig. 63.1-3. – ONYMOTOPE: Mengyang (21°37'N, 101°22'E), Xishuanbanna Daizu Zizhizhou, Yunnan Sheng, China. – STATUS: **New synonym**.

Sylvirana cubitalis, first described by SMITH (1917) from Myanmar (fig. 4), is a frog species with a large distribution in northern Thailand. The males are easily recognized because they have a prominent glandular patch of nuptial spines on the forearm unique among ranine frogs. For thirty years, the Philippine species *Rana varians* Boulenger, 1894 was considered to occur in southern China. On morphological data, particularly on the difference in tadpole mouth structure, DUBOIS (1992) distinguished the Chinese form as *Rana nigrotympanica* (fig. 5a). This species was only known from three female specimens (LIU & HU, 1961; YANG, 1991*a*). Description of holotypes of these two nominal species will be published elsewhere (OHLER & DUBOIS, in prep.). STUART et al. (2006) published a redescription of this frog from northern Laos as *Rana nigrotympanica* and compared it briefly with *Rana cubitalis*. In the specimens they studied, vocal pouches are absent.

Recent collections in northern Laos adjacent to the onymotope of *Rana nigrotympanica* included a frog species whose females fit with the Chinese form in having a distinct dark triangle at the tympanic region, but the males have the sexual characters of *Rana cubitalis* (fig. 6). Morphometrical data on Lao specimens and types are given in table 5 and support similarity of the frogs from different populations. Though there is variation in size, the observed values for RE are not particularly high (♂ RE = 1.30, ♀ RE = 1.32). As

Fig. 3. – *Pelophylax lateralis* (Boulenger, 1887). Specimens in dorsal view. (a) Left, dark coloured specimen with oblique bands, MNHN field number Y.0041, ♂, SVL 53.2 mm. Right, light coloured specimen without bands, MNHN field number 17543, ♀, SVL 58.8 mm. Both specimens from Phitsanulok Province, Thailand. (b) Holotype of *Rana nigrolineata* LIU & HU, 1959, CIB 571085, ♂, SVL 50.5 mm; Mengyang, Yunnan, China.

Source : MNHN, Paris

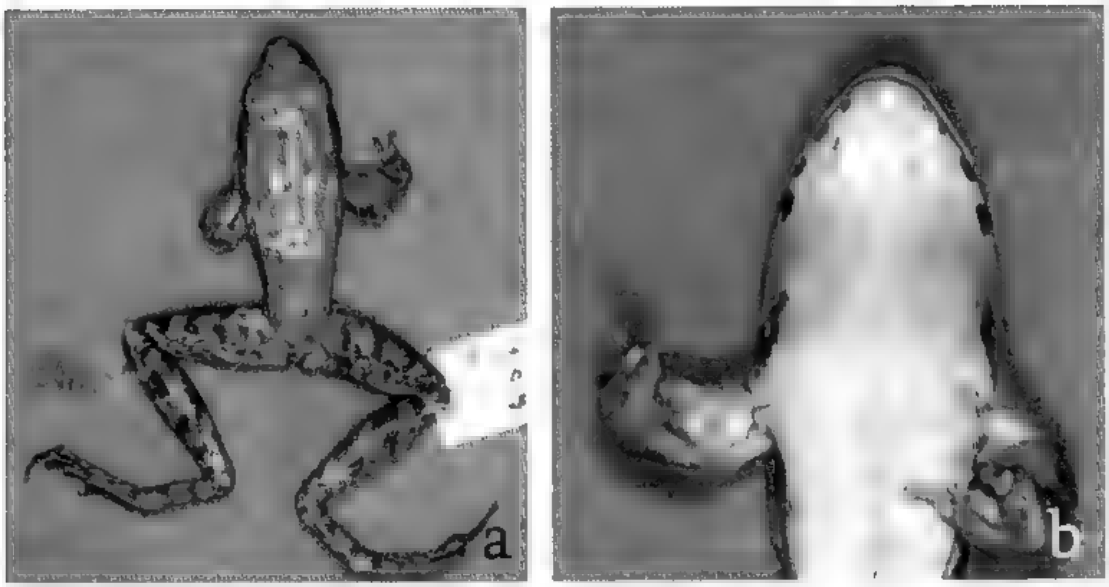


Fig. 4 — *Sylvirana cubitalis* (Smith, 1917). Holotype of *Rana cubitalis* Smith, 1917, BMNH 1947.2.2.35, ♂, SVL 66.8 mm, Doi Nga Chang, Thailand. (a) Dorsal view. (b) Ventral view of throat and right forearm showing glandular pad.

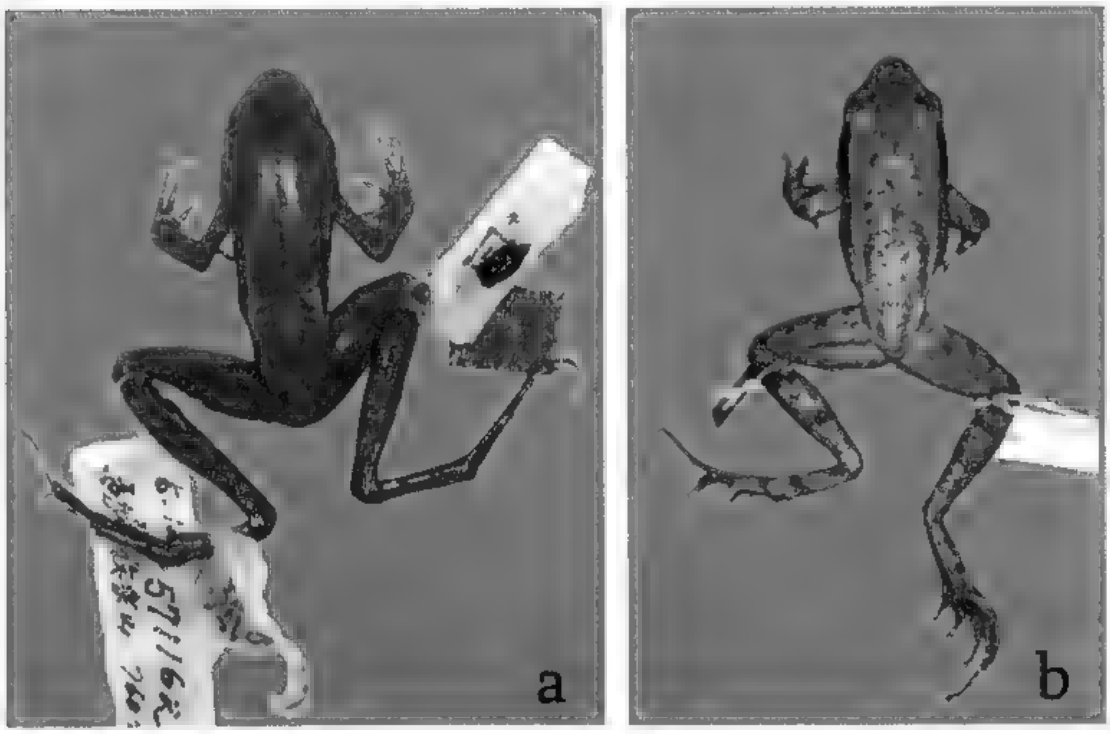


Fig. 5 — (a) *Sylvirana cubitalis* (Smith, 1917). Holotype of *Rana* (*Sylvirana*) *nigrotympanica* Dubois 1992, CIB 571162, ♂, SVL 61 mm, Mengyang, Yunnan, China, dorsal view. (b) *Sylvirana mitleti* (Smith, 1921). Syntype of *Rana mitleti* Smith, 1921, BMNH 1947.2.1.45 [ex MAS 2602], ♂, SVL 36.2, Da Lat, Lam Dong Province, Vietnam; dorsal view.

Source : MNHN, Paris

Fig. 6. (a) *Sylvirana cubitalis* (Smith, 1917), MNHN 2005.0224, ♂, SVL 52.4 mm, Long Nai, Phongsaly Province, Laos, specimen in life. (b) *Sylvirana milleti* (Smith, 1921), MNHN 2004.0370, ♂, SVL 40.3, Long Mai Khao, Phongsaly Province, Laos; specimen in life.

morphological data are available only on small samples of this species (21 ♂, 10 ♀), conclusions on variation must be prudent. In specimens collected in Phongsaly Province (MNHN 2005.0224-0230), adult males have more or less distinct foldings on sides of throat but no extended vocal pouch. In the male specimens described by STUART et al. (2006), vocal pouches were absent. SMITH (1917) described these pouches as external, whereas BOULENGER (1920: 139), BOURRET (1942: 317) and TAYLOR (1962: 426) mentioned internal vocal sacs. Study of the type specimens (BMNH 1947.2.2.36 [ex MAS 1106] and 1921.4.1.229 [ex MAS 2107]) confirms the vocal pouches being internal without morphological modification on throat (fig. 4b). Thus the description of SMITH (1917) is wrong and does not

Source : MNHN, Paris

Table 5. Measurements of *Sylvirana cubitalis* (Smith, 1917), including type specimens of *Rana cubitalis* Smith, 1917, holotype of *Rana (Sylvirana) nigrotympanica* Dubois, 1992 and other specimens allocated to this taxon. Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the Yunnan specimens of *Rana nigrotympanica* which are from YANG (1991*a*).

Measurement	*Rana cubitalis*			
	Myanmar		Thailand	
	Holotype ♂ *n* = 1	Paratype ♂ *n* = 1	♂ *n* = 3	♀ *n* = 4
SVL	66.8	64.8	55.2-67.8	60.7-75.2
HW	20.8	18.3	15.6-20.9	19.1-22.1
HL	23.2	21.0	20.1-24.5	22.9-26.5
TL	39.1	37.4	29.5-40.7	35.5-42.6
Measurement	*Rana nigrotympanica*			
	Yunnan		Laos	
	Holotype ♀ *n* = 1	♀ *n* = 2	♂ *n* = 4	♀ *n* = 3
SVL	57.1	63.5-65	51.4-57.2	59.4-66.6
HW	18.2	19-19.5	14.7-16.8	18.6-19.8
HL	21.0	21.5-22	19.1-20.4	21.9-23.5
TL	35.3	37-39	29.8-34.0	34.0-39.1

provide a discriminant character as supposed by STUART et al. (2006). In conclusion, the name *Rana nigrotympanica* refers to the female of *Rana cubitalis*, and the name *Rana nigrotympanica* is a junior subjective synonym of *Rana cubitalis*, with *Sylvirana cubitalis* as its valid name.

Sylvirana milleti (Smith, 1921)

Rana milleti Smith, 1921: 431. HYPODIGM: 5 ♂, 5 ♀. ONOMATOPHORE: Syntypes, BMNH 1947.2.1.37-46, 5 ♂, 5 ♀, SVL respectively 35.0-37.9 mm and 44.4-47.8 mm. ONYMOTOPE: Da Lat [Dalat] (11°58'N, 108°24'E), Langbian Plateau, Lam Dong Province, Vietnam.

Rana hainanica Rao & Yang, 1997: 157. HYPODIGM: 8 ♂. ONOMATOPHORE: Holotype, by original designation, KIZ 94001, ♂, SVL 43.0 mm. ONYMOTOPE: Mo-han (21°10'N, 101°45'E, alt. 850 m), China-Laos border, Xishuangbanna Dai'zu Zizhizhou, Yunnan Sheng, China. STATUS: **New synonym**.

SMITH (1921) described *Rana milleti* from the Lang Bian Plateau of central Vietnam (fig. 5b). The species was known only from this region until the recent discovery of the species

Source : MNHN, Paris

Table 6. - Measurements of *Sylvirana milleti* (Smith, 1921), including type specimens of *Rana milleti* Smith, 1921 and of *Rana bannanica* Rao & Yang, 1997, and other specimens allocated to this taxon. Measurements (minimum-maximum) are given in millimetres. Measurements are original except for those of the type specimens of *Rana bannanica* which are from RAO & YANG (1997)

Measurement	*Rana milleti*			
	Vietnam		Thailand	
	Syntypes ♂ *n* = 5	Syntypes ♀ *n* = 5	♂ *n* = 14	♀ *n* = 1
SVL	35.0-37.9	44.4-47.8	38.3-41.7	49.4
HW	12.3-12.8	14.4-15.5	11.3-12.9	15.7
HL	13.2-14.2	16.6-18.5	14.6-16.1	18.8
TL	18.9-20.3	24.2-26.4	21.0-23.2	26.7
Measurement	*Rana bannanica*			
	Yunnan		Laos	
	Holotype ♂ *n* = 1	Paratypes ♂ *n* = 7	♂ *n* = 6	♀ *n* = 1
SVL	43.0	38.0-43.0	37.5-41.1	45.6
HW	14.0	12.0-14.0	12.0-13.5	14.7
HL	17.0	15.0-17.0	15.1-16.1	17.5
TL	22.0	20.0-23.0	18.7-22.9	23.9

from Thailand and Cambodia (CHUAYNKERN et al., 2004). In 1997, RAO & YANG described a brown *Rana* similar to *Rana nigrovittata* from the China-Laos border.

When doing field work in Phongsaly province of Laos, near to the Chinese border, I discovered a small brown frog (fig. 6b) which corresponds in morphological characters closely to the description of *Rana bannanica*, but also to the type specimens and other specimens studied of *Rana milleti*. These two forms are the only *Sylvirana* that share the following characters: small body size, moderately large head, reduced webbing, dorsal skin bearing glandular warts and dense horny spinules. Morphological analysis shows no major differentiation but a slightly smaller size in the syntypes from Vietnam (tab. 6), but size variation is of small or moderate amplitude (♂ RE = 1.23, ♀ RE = 1.11). Smaller size is not correlated to any other character of shape, morphology or coloration. Pending genetic data, *Rana bannanica* should be regarded a junior subjective synonym of *Rana milleti*, with the valid name *Sylvirana milleti*. The distribution area of the species is extended far north to southern Yunnan. Rarity of records may be due to problems of taxonomic allocation (some specimens could be regarded as juveniles of "*nigrovittata*") but also due to ecological demands. Specimens have been collected in marshes and ponds close to forests or in primary

Source : MNHN, Paris

forest. As pointed out by OHLER & DELORME (2006), this kind of habitats is particularly rare in Asia as most of lowland forests and forests on non-sloping parts have disappeared to be replaced by paddies.

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Source : MNHN, Paris

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APPENDIX 1

SPECIMENS STUDIED

Amolops mengyangensis. CHINA: Yunnan Sheng, Mengyang, CIB 579034, CIB 579037, CIB 64.1.1901, ♂. VIETNAM: Lao Cai Province, Sa Pa, MNHN 1999.5799-5813, ♂.

Odorrana jingdongensis. VIETNAM: Lao Cai Province, Sa Pa, MNHN 1938.0054-0057, MNHN 1999.5762-5781, topotypes of *Rana hmongorum*, ♂, ♀, juv.

Odorrana tiannanensis. LAOS: Phongsali Province, Nathen, MNHN 2004.0408, ♀, Houey Phihet, MNHN 2005.0180-0188, ♂.

Pelophylax lateralis. CHINA: Yunnan Sheng, Mengyang, CIB 571085, holotype of *Rana nigrolineata*, ♂, CIB 570392, paratype of *Rana nigrolineata*, ♀. LAOS: Vientiane market, MNHN 1997.4079-4088, ♂, ♀. MYANMAR: Rangoon, BMNH 1893.10.9.16, ♂, MNHN 1893.0456, ♂. THAILAND: Phitsanulok Province, Nam Pad District, MNHN field number Y0041-0044, ♂, ♀.

Sylvirana cubitalis. LAOS: Phongsali Province, Long Mai Kao, MNHN 2005.0224-0227, ♂, ♀, Nathen, MNHN 2005.0228, ♂, Houey Phihet, MNHN 2005.0229, ♀, Ban Phoumouang, MNHN 2005.0230, ♀. THAILAND: "Doi Nga Chang", BMNH 1947.2.2.36, holotype of *Rana cubitalis*, ♂, BMNH 1921.4.1.229, ♂, FMNH 135341-2, ♂, ♀; Loei Province, Dansai District, FMNH 196016, ♀, FMNH 125017, ♂, Chiang Mai, FMNH 173953, ♀, FMNH 125945, ♂, FMNH 51288, ♀.

Sylvirana milleti. LAOS: Phongsali Province, Long Nai, MNHN 2004.0370-0376, ♂, ♀. THAILAND: Khao Yai, MNHN 1987.3433-3444, ♂. VIETNAM: Langbian Plateau, BMNH 1947.2.1.37-46, syntypes of *Rana milleti*, ♂, ♀.

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Source : MNHN, Paris

The status of the nomen *Rana (Paa) dhakuriensis* Ray, 1997 (Anura, Ranidae), and comments on the Amphibia reported from the Nanda Devi Biosphere Reserve (Uttar Pradesh, India)

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The nomen *Rana (Paa) dhakuriensis* Ray, 1997 was published without any character allowing to recognize the taxon and is therefore a nomen nudum. The status of the Amphibia reported by RAY (1997) from the Nanda Devi Biosphere Reserve, under this nomen and seven others, is briefly discussed.

DUBOIS et al. (2005: 45) included the nomen *Rana dhakuriensis* Ray, 1997 in their list of recent amphibian taxonomic additions, without having had the opportunity to see the original publication where this nomen had been created. Examination of this paper shows that this new nomen was proposed for a taxon that was not described or diagnosed in any way. Here is an integral copy of the part of this text dealing with this purported new species: "Morphologically differs from all other species known from the neighbouring areas. Cryptic colouration perfectly camouflaged these individuals with the natural surroundings. Detailed description will be published after thorough study of the material". There is in this text no "description or definition that states in words characters that are purported to differentiate the taxon", or mention of "a bibliographic reference to such a published statement", so that this nomen is a nomen nudum according to Article 13.1 of the *Code* (ANONYMOUS, 1999). One could at first sight consider "cryptic coloration" as a "character" of the species, but it is not, as would be mention of a colour (brown, green, etc.): it is just an interpretation of what in the eyes of a human this frog looks like, but it does not describe it. We are not aware that any "detailed description" of this taxon was published later on, so that this nomen has no status in zoological nomenclature. The question may arise, however, for which taxon was this new nomen coined, and in which synonymy, if any, should the latter be placed. As Pranjalendu

Source : MNHN, Paris

Ray does not seem to have commented again on the Nanda Devi amphibian fauna in subsequent works, and as the specimens are presumably kept in the Dehra Dun station of the Zoological Survey of India which we did not have the opportunity to visit, all we can do is to start from the information provided in RAY (1997).

To the best of our knowledge, the Amphibia of the Nanda Devi Biosphere Reserve Park (Uttar Pradesh, India; quite close to the western border of Nepal) had never been studied before the work of RAY (1997), so that a priori one could consider plausible the discovery of a new species in this area But this possibility is slight, regarding the uncertainties of the taxonomy of amphibians used in this publication, as shown below Based on collections including 13 adults, one juvenile and 349 tadpoles, RAY (1997) reported 8 species from this reserve, under the following nomina: (1) *Bufo himalayanus* Günther, 1864; (2) *Bufo melanostictus* Schneider, 1799; (3) *Megophrys* sp., (4) *Amolops* sp.; (5) *Rana (Paa) annandalii* Boulenger, 1920, (6) *Rana (Paa) blanfordii* Boulenger, 1882; (7) *Rana (Paa)* sp., (8) *Rana (Paa) dhakuriensis* n sp. We comment below on these reports following the generic taxonomy

Bufo Laurenti, 1768

The presence of the two species of *Bufo* reported by RAY (1997) is likely in this area, as both these species occur in Nepal (DUBOIS, 1976, 1980, 1981, 2000) and in the Indian western Himalayas as far West as Jammu and Kashmir (DUBOIS & MARTENS, 1977, DUBOIS, 1980, 1981). The brief notes of RAY (1997) suggest that his identification of the specimens was correct.

According to the proposals of DUBOIS (1988, 2004*b*), in zoology two species liable to hybridize successfully, either in the field or in artificial conditions, and to provide genuine adult hybrids (at least in some cases), should never be allocated to different genera (but may be placed in different subgenera). Adopting this point of view, we cannot follow the suggestion of FROST et al. (2006) to dismantle the genus *Bufo* into several genera between which some species are known to hybridize (BLAIR, 1972). For example, successful hybridization until the adult stage is known to occur (at least in some cases, as "best result") between species belonging in FROST's et al. (2006) genera *Anaxyrus* Tschudi, 1845 and *Bufo* Laurenti, 1768 (e g , *Bufo bufo* and *Bufo woodhousii*, see BLAIR, 1972: 420), *Anaxyrus* and *Cranopsis* Cope, 1875 (e g , *Bufo terrestris* and *Bufo valliceps*, see BLAIR, 1941 and MOORE, 1955, or *Bufo fowleri* and *Bufo valliceps*, see BLAIR in MOORE, 1955), *Bufo* and *Pseudepidalea* Frost et al , 2006 (e g , *Bufo bufo* and *Bufo viridis*, see HEMMER & BÖHME, 1974), *Epidalea* Cope, 1864 and *Pseudepidalea* (e g , *Bufo calamita* and *Bufo viridis*, see FLINDT & HEMMER, 1967, HEMMER, 1973, SCHLYTER et al., 1991). It also probably occurs between *Bufo* Laurenti, 1768 and *Epidalea* Cope, 1864 (*Bufo gargarizans* [as *asiaticus*] and *Bufo raddei*, according to CHEN, 1940), if, as suggested by the data of STOCK et al (2001), the species *Bufo raddei* belongs indeed in the *Epidalea* group rather than in the *Pseudepidalea* group as tentatively proposed by FROST et al (2006). According to the cladogram of FROST et al (2006 218), following DUBOIS's (2004*b*) guidelines and in order not to recognize paraphyletic genera, placing *Bufo bufo* and *Bufo viridis* in the same genus requires to include also in the latter not only all other species of FROST et al 's (2006) genera *Bufo* and *Pseudepidalea*, but also all species of their genera *Amietophrynus*, *Anaxyrus*, *Chaunus*, *Cranopsis*, *Duttaphrynus*, *Epidalea*, *Mertensoi-*

Source : MNHN, Paris

phryne, *Peltophryne* and *Vandijkophrynus*. It is however possible, if one wishes to recognize taxonomically these "subclades" as taxa, to give them the status of subgenera of the genus *Bufo*. Under this arrangement, the two indian species mentioned above can be referred to the subgenus *Duttaphrynus* Frost et al , 2006 (type-species by original designation *Bufo melanostictus* Schneider, 1799) and can therefore be known as *Bufo (Duttaphrynus) himalayanus* Günther, 1864 and *Bufo (Duttaphrynus) melanostictus* Schneider, 1799. Another advantage of this solution is that it does not require to change the well-known binomen of the latter species (*Bufo melanostictus*), one of the most quoted nomina of amphibians in the world, being one of the commonest species in Asia

Xenophrys Günther, 1864

The use of the generic nomen *Megophrys* Kuhl & Van Hasselt, 1822 is now restricted to frogs of the Sunda islands, and the related species of the Himalayas are now referred to the genus *Xenophrys* Günther, 1864 (FROST et al., 2006, DELORME et al., 2006) A single species of this genus, *Xenophrys parva* (Boulenger, 1893), is known to occur in the western part of Nepal. The westernmost locality for which referenced voucher specimens have been reported so far (DUBOIS, 1974) is Ghasa (28°37'N, 83°38'E, alt 2050-2100 m). In ANDERS's (2002: 167) distribution map of the species, a dot indicates its presence in a locality of the extreme western part of the country, close to the border of Uttar Pradesh, but as the book of SCHLEICH & KÄSTLE (2002) provides no reference to collection numbers of voucher specimens examined, and as the amphibian taxonomy used in this book is not reliable (as it contains gross misidentifications of specimens, see DUBOIS, 2004*a*), the validity of this record is open to question. Regarding the specimens from the Nanda Devi reported by RAY (1997: 110), they are stated to consist in "one hundred forty tadpoles of different stages" and mention is made of their "Funnel type mouth feeding from the surface material and tail flickering continuously under water", a brief description which clearly points, indeed, to a species of the genus *Xenophrys* Pending obtention of adults from this area, the most parsimonious attitude is to refer these specimens to *Xenophrys parva*. This is a genuine addition to the amphibian fauna of Uttar Pradesh, and indeed an important range extension to the West, not only for this species, but also for the genus *Xenophrys* and for the subfamily Megophryinae as defined by DELORME et al (2006).

Amolops Cope, 1865

In contrast, the genus *Amolops* has long been known from the western Himalayas (ACHARJI & KRIPALANI, 1951, KRIPALANI, 1952) It is represented there by at least two distinct species, now known (DUBOIS, 1974, 1992, 2000) as *Amolops formosus* (Günther, 1875) and *Amolops marmoratus* (Blyth, 1855) Both these species are present from eastern to western Nepal (DUBOIS, 1974, 1976, 2000) and in the western Himalayas as far west as Himachal Pradesh (DUBOIS, 1981) A third species of this genus, *Amolops monticola* (Anderson, 1871), is known from eastern Nepal but has not yet been reported in this country west of the Arun valley (DUBOIS, 1980) The material from Nanda Devi reported by RAY (1997) consists in 13

Source : MNHN, Paris

tadpoles with ventral abdominal sucker, which therefore most likely belong in this genus, but specific allocation is unknown. In another work on the amphibians of the Dehra Dun district (Uttar Pradesh), RAY (1992) described two new species: *Amolops chakrataensis* (apparently very similar to *Amolops monticola*) and *Amolops jaunsari* (apparently quite similar to *Amolops marmoratus*). Both these species were redescribed as new by RAY (1999), in a paper erroneously considered to provide their original descriptions by DUBOIS et al. (2005). The validity of both these species will have to be confirmed by comparative studies in the frame of a comprehensive revision of the genus *Amolops*, which is badly needed to solve the problems left aside or created by the work of YANG (1991) on this genus. Although tadpoles of these frogs can rather easily be collected in large numbers, e.g. by drying up portions of the torrents where they live, adults are usually nocturnal, secretive, and they rarely leave the torrent bed: to find them in significant numbers one has to climb slowly within the bed of the torrent at night with head lamps or torchs. They are therefore quite seldom collected during standard surveys of amphibians which are often made mostly around villages, in open habitats like paddy fields, and at day time. Thus, these frogs are poorly known, and herpetologists who incidentally collect them may consider them as new without making appropriate comparisons. Combined with the rather high intraspecific variability of several species of this genus, this probably explains the existence of many synonyms for some of them, including *A. formosus* and *A. marmoratus* (DUBOIS, 1974, 2000), and ignoring some of these synonymies without providing new data, as done by some recent authors (YANG, 1991, ANDERS, 2002; FROST et al., 2006) is not likely to help our understanding of the taxonomy of this genus (see appendix 1).

Chaparana Bourret, 1939

The most problematic aspect of the paper of RAY (1997) is the taxonomy used for the frogs referred to the subgenus *Rana* (*Paa*), including the so-called new species. This subgenus is now included in the genus *Chaparana* Bourret, 1939 (OHLER & DUBOIS, 2006), and it has been the matter of several important works since the monography of BOULENGER (1920) which seems to have been used as the basic taxonomic reference for RAY's (1997) work.

Neither species *Chaparana annandalii* (Boulenger, 1920) and *Chaparana blanfordii* (Boulenger, 1882) can be present in the Nanda Devi region. These are East Himalayan species, which both occur only east of the Arun valley in eastern Nepal, in north-eastern India, and, only for the second species, Bhutan (DUBOIS, unpublished) and southern Xizang (Tibet) in China (DUBOIS, 1976, 1979, GROSJEAN & DUBOIS, 2006).

RAY's (1997) report of *Rana blanfordii* in the reserve was based on 7 "examples" (adults?) and 73 tadpoles, but no diagnostic characters were mentioned allowing to support their identification. The specimens from Mussoorie (now in Uttar Pradesh) and the Balaya valley near Simla (now in Himachal Pradesh) referred by BOULENGER (1920: 84) to *Rana blanfordii* were shown by DUBOIS (1975, 1976) to be members of the species *Chaparana minica* (DUBOIS, 1975). This is a small species (SVL: ♂ 28.5-35.0 mm, ♀ 30.5-41.0 mm, DUBOIS, 1976), which could possibly be mistaken for *Chaparana blanfordii* (SVL: ♂ 36.0-40.5 mm, ♀ 41.0-48.0 mm, DUBOIS, 1976). The occurrence of *C. minica* is likely in the Nanda Devi region, since it was reported both east and west of the Park (DUBOIS, 1976, 1992, THAK & RAY, 1985, as *Rana* (*Paa*) *tuberculata*), but it only occurs at rather low altitudes (1000-2440 m, DUBOIS, 1976), so

Source : MNHN, Paris

it may only be present in the lowest parts of the Park whose elevation range spreads from 1500 to 5600 m.

RAY's (1997) report of *Rana annandalii* in the Nanda Devi was based on a single juvenile, and its identification was stated to be "based on descriptive morphology described by BOULENGER (1920)", without further details. *Chaparana annandalii*, which has never been reported from west of Nepal, is similar in size to *C. blanfordii* or a little larger (SVL ♂ 32.5-51.5 mm, ♀ 40.0-50.5 mm, DUBOIS, 1976). It could possibly be confounded with *Chaparana rarica* (Dubois, Matsui & Ohler, 2001), which is of similar size (SVL ♂ 37.3-45.6 mm, ♀ unknown) and rather similar aspect (DUBOIS & MATSUI, 1983). For the time being, the latter is known with certainty only from one locality in western Nepal, the lake Rara (29°31'N, 82°05'E; alt. 2990 m). The second locality mentioned by ANDERS (2002: 285, 1052), Gurja Ghat, is based on 7 specimens referred with doubts to this species by NANHOE & OUBOTER (1987), the status of which is not clear. The discovery of this species in Uttar Pradesh would be an interesting range extension and would add one species to the fauna of India.

Beside the two species above, RAY (1997) reported two other samples of *Paa* from the Nanda Devi reserve: 100 tadpoles as *Rana* (*Paa*) sp., and 6 "examples" (adults?) as "*Rana* (*Paa*) *dhakuriensis*" (nomen nudum). Could these specimens represent still one or two other species of *Chaparana*?

Three other species of *Chaparana* have been reported so far from the regions neighbouring the reserve. *Chaparana vicina* (Stoliczka, 1872), *Chaparana polunini* (Smith, 1951) and *Chaparana ercepeae* (Dubois, 1974). *Chaparana vicina* is known from northern Pakistan, Jammu & Kashmir and Himachal Pradesh (DUBOIS, 1980, GROSJEAN & DUBOIS, 2006), and its finding in the Nanda Devi would be an important range extension to the East. *Chaparana polunini* has so far been reported only from Nepal, from the East (west of the Arun valley) to the extreme West of the country (DUBOIS, 1976), and from southern Xizang (China), at altitudes between 2610 and 3990 m (DUBOIS, 1979). Its discovery in the Nanda Devi would be a modest extension of its range to the West, but a new species record for India. Finally, *Chaparana ercepeae* is known only from the extreme West of Nepal, between 2200 and 2650 m (DUBOIS, 1976; DUBOIS & MATSUI, unpublished), and its presence in the Nanda Devi is also quite possible, but would also be a new record for India. Finally, ANDERS (2002: 275) also reported another species, *Chaparana liebigii* (Gunther, 1860) from extreme western Nepal, but this record is highly open to question and might be based on a confusion with *Chaparana ercepeae*. The westernmost locality known with certainty for *C. liebigii* and based on an identified voucher is Lumsum (28°31'N, 83°17'E ; alt. 1980-2130 m) in central-western Nepal (DUBOIS, 1976: 259).

In conclusion, the region of the Nanda Devi Reserve Biosphere, in medium and high altitude just west of the occidental border of Nepal, certainly harbours frogs of the genus *Chaparana*. The species *C. minica*, present both to the West and to the East of the reserve, is most likely present in the latter. Three other species, *C. ercepeae*, *C. polunini* and *C. rarica*, present in western Nepal, could possibly occur there, whereas, given geographic distance, the presence of *C. vicina* is more unlikely. At any rate, before describing a new species of *Chaparana* from this area, careful comparisons of specimens collected there, including those used to create the nomen "*Rana dhakuriensis*", should be done with reliably identified

Source : MNHN, Paris

specimens of these five species. Until such a work can be carried out, we suggest to place provisionally the latter nomen nudum, with a query, in the synonymy of *Chaparana minica*, together with the nomen *Rana tuberculata* Tilak & Ray, 1985 (see DUBOIS, 1992: 339).

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APPENDIX 1
MISCELLANEOUS TAXONOMIC COMMENTS ON THE GENUS *AMOLOPS*

Some of the current taxonomic problems pointed out above in the genus *Amolops* simply came from quick and careless reading of the works of colleagues, as exemplified in several cases below.

Source : MNHN, Paris

(1) YANG (1991: 16) wrote: "Dubois (1974) suggested *A. kaulbacki* is probably a subspecies of *A. afghanus*", whereas DUBOIS (1974: 361) had suggested that *A. kaulbacki* might be a subspecies of *A. formosus*.

(2) YANG (1991) completely ignored the synonymisation by DUBOIS (1974) of *A. himalayanus* with *A. formosus*, although it was based on statistical comparisons of series of specimens. YANG (1991), followed by FROST et al. (2006: 367), recognized both species but did not even compare them in their respective diagnoses.

(3) Quite similarly, FROST et al. (2006: 252) wrote: "Dubois (2000: 331; 2004a: 176) suggested, on the basis of the examination of the holotype, this taxon [*Amolops nepalicus*] is synonymous with *Amolops formosus*", whereas DUBOIS (2000: 333, 335) had considered *A. nepalicus* a synonym of *A. marmoratus*. Such gross misquoting testify to poor attention given to the publications at stake.

(4) FROST et al. (2006: 252) further complained that "[Dubois] did not provide any discussion regarding the differences itemized in the original description or the diagnostic differences noted by Yang (1991b)". Beside the absence of meaning of "or" in this sentence (as the original description of *A. nepalicus* was indeed in YANG, 1991), this statement is misleading, as *a single* difference was stated by YANG (1991: 23) to distinguish *A. nepalicus* from *A. afghanus* (now *A. marmoratus*): "*A. nepalicus* differs (...) from *A. afghanus* in having the vomerine tooth groups oblique instead of transverse", which, to experienced taxonomists nowadays, is at least a doubtful criterion for species recognition. The description of *A. nepalicus* from *a single* adult male and 5 tadpoles (without any information on their locality data and on the reasons for their allocation to the same species as the adult male), without any morphological or statistical comparison with the many adults of *A. marmoratus* available from Nepal (e.g., 39 ♂, 9 ♀, 7 juveniles and 14 tadpoles listed in DUBOIS, 1974: 397-398), looks more like a 19th century's typological description, ignoring intraspecific variability, than like a recent taxonomic work, and it is surprising to see subsequent support for such a hasty work (ANDERS, 2002; FROST et al., 2006).

(5) Instead of "resurrecting" specific synonym nomina without any evidence (e.g., *A. himalayanus* and *A. nepalicus*, but also *Rana barmoachensis* Khan & Tasnim, 1979, synonymized with *R. hazarensis* by DUBOIS, 1992), FROST et al. (2006) could have cared for presenting a consistent generic taxonomy of frogs of this complex. It is thus difficult to understand on which basis they put some species in two different genera, although at least morphologically they are very similar and appear very closely related (e.g., *Rana monticola* Anderson, 1871 (placed by them in *Amolops* Cope, 1965) and *Rana archotaphus* Inger & Chan-ard, 1997 (placed by them in *Hina* Yang, 1991, but which should probably rather be known as *Amolops archotaphus*).

(6) As explained by DUBOIS (2004*a*), the specimens referred by ANDERS (2002) to *Amolops monticola* are in fact *Amolops formosus*, whereas they described their specimens of *Amolops monticola* as "*Polypedates* species, not identified".

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Source : MNHN, Paris

Provenance de trois espèces de *Phrynobatrachus* d'Afrique centrale décrites par Ahl en 1925 (Anura, Ranidae)

Thierry Frétey

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The precise origin of the specimens described by Ahl (1925) as three new species is shown to be Bouala in République centrafricaine.

Ahl, en 1925, a décrit trois espèces nouvelles: *Hylarthroleptis elberti* (17 syntypes), *Pararthroleptis nanus* (1 seul spécimen, holotype par monotypie) et *Arthroleptis pygmaeus* (1 seul spécimen, holotype par monotypie) qui ont été transférées depuis dans le genre *Phrynobatrachus* Gunther, 1862 (Dubois, 1981)

Ces trois nouvelles espèces proviennent de "Buala am Uam, Neu Kamerun". En 1985, Frost, dans son ouvrage de référence, citait donc tout simplement comme localité-type "Buala am Uam, Neu Kamerun" : du Cameroun. Depuis 2004, dans la version 3, et en 2006, dans la version 4, de "Amphibian Species of the World" sur le site internet de l'American Museum of Natural History [http://research.amnh.org/herpetology/amphibia/], Frost a modifié cette localité-type en "Buala am Uam, Neu Kamerun" : du Tchad.

Sur une carte du Tchad, aucune localité "Buala am Uam" ne figure. En revanche, il existe une rivière "Ouham" qui coule au Tchad avant de se jeter dans le Chari. Or, cette rivière prend sa source en République centrafricaine. Sur des cartes détaillées, nous avons pu retrouver la localité dénommée "Bouala" (06°22'N, 15°37'E; altitude 998 m) en remontant le cours du "Ouham", à 45 km au nord de Bouar, en République centrafricaine et à moins de 60 km de la frontière camerounaise (fig. 1).

L'histoire du Cameroun, au début du siècle dernier, est en effet assez tourmentée : en 1911, ce pays, alors colonie allemande dénommée "Neu Kamerun", englobait, au Sud et à l'Est, des régions du Gabon, du Congo, du Tchad et de la République centrafricaine actuels, cédées par la France. Ce n'est qu'en 1919, après la guerre, que ces territoires ont réintégré l'Afrique équatoriale française (fig. 2).

La localité-type ou onymotope (Dubois, 2005) de *Phrynobatrachus elberti*, *P. nanus* et *P. pygmaeus* est donc en fait en République centrafricaine.

Source : MNHN, Paris

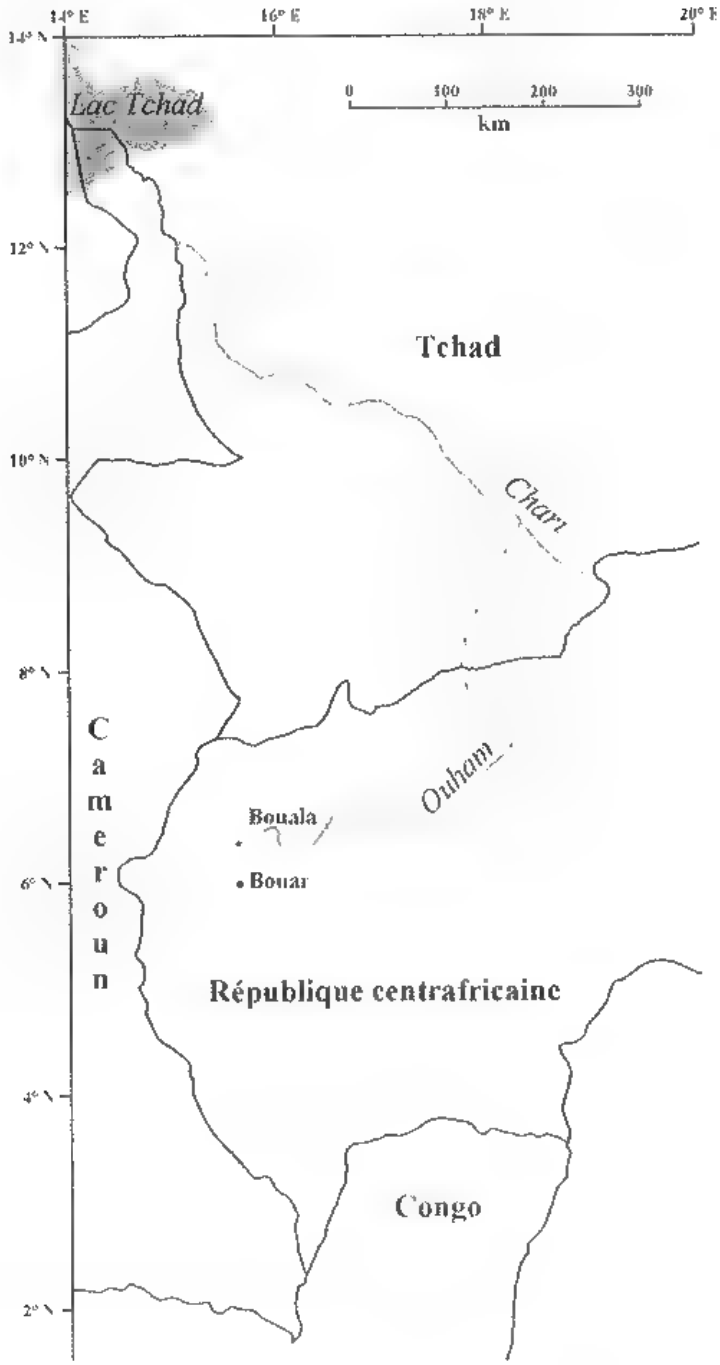

Fig. 1 – Carte de localisation de Bouala, République centrafricaine

Source : MNHN, Paris

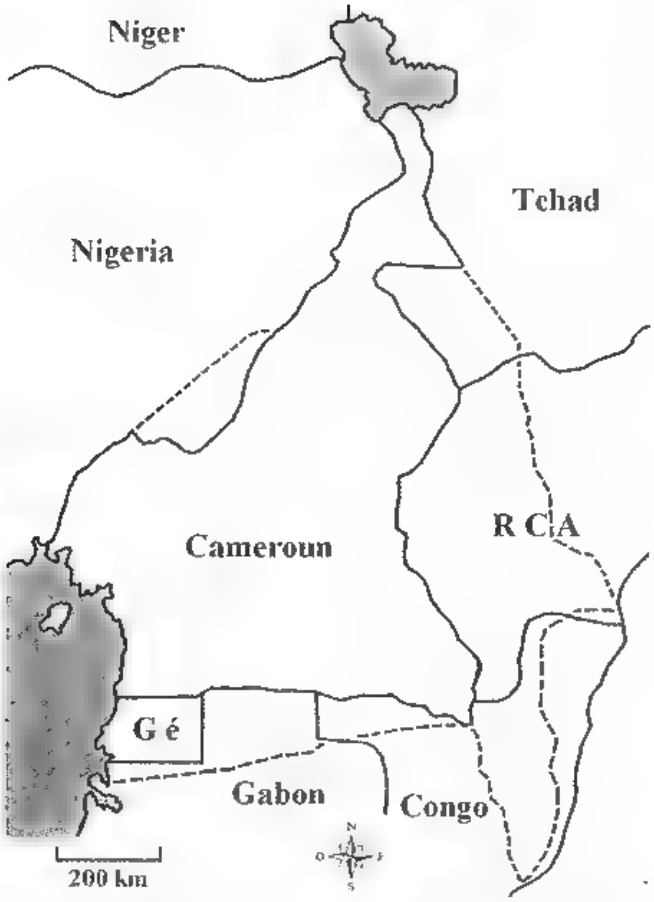

Fig 2 Carte du "Neu Kamerun" entre 1911 et 1919 En trait plein . frontieres actuelles des differents pays. En trait pointile frontières du "Neu Kamerun" entre 1911 et 1919. G é, Guinee equatoriale, RCA, République centrafricaine.

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The publication date of the book *Key to Chinese Amphibia* by Fei, Ye & Huang

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** Chongqing Nature Museum, Chongqing 400700, China

The book *Key to Chinese Amphibia*, by Fei Liang, Ye Changyuan and Huang Yongzhao, has sometimes be quoted as having been published in 1991. As shown by an official certificate here reproduced, this is wrong, as it was published in China in December 1990.

The book *Key to Chinese Amphibia*, by FEI Liang, YE Changyuan and HUANG Yongzhao was a landmark in the history of Chinese batrachology. It was the first comprehensive list of the amphibians of China published after the *Systematic key to the Amphibians of China* published in 1977 by the Sichuan Institute of Biology (ANONYMOUS, 1977). It provided keys, diagnoses and figures for the adults, larvae and eggs of 279 species, arranged in 58 genera and subgenera and in 11 families and subfamilies, and it gave the distribution of these species in the provinces of China. It contained the creation of 15 new nominal taxa: 6 species (*Leptolalax alpinus*, *Leptolalax liui*, *Leptolalax ventripunctatus*, *Megophrys glandulosa*, *Megophrys mangshanensis*, *Oreolalax granulosus*), 5 genera (*Glandirana*, *Odorrana*, *Pseudorana*, *Rugosa*, *Tigrina*), 3 subgenera (*Quadrana*, *Tenurana*, *Unculuana*) and 1 subfamily (Occidozyginae).

In the second, unnumbered, page of the book (p. [ii]), the date of the book was given as 1.12.1990 (1st December 1990). The book was distributed first in China in December 1990, then mailed free to various colleagues in the world, but was apparently received there only several weeks after the beginning of the year 1991. Probably for this reason, ZHAO & ADLER (1993: 367) credited this book with the publication year 1991 instead of 1990. This information was repeated in several works, especially in FROST et al. (2006: 253, 266), who furthermore wrote that "this publication did not appear until at least March of 1991" (FROST et al., 2006, 253).

This latter information is wrong, as shown by the official certificate reproduced here in figure 1, and which can be translated as follows:

"Certificate

We formally here certify that the book *Key to Chinese Amphibia* by Fei Liang, Ye Changyuan and Huang Yongzhao was published in fact in December 1990 by the Chongqing branch of the Science and Technology Literature Publishing House.

Source : MNHN, Paris

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30 September 2006."

The book should therefore be quoted as FEI, YE & HUANG (1990), and the new taxa named therein are dated December 1990.

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INGER, R. F., VORIS, H. K. & VORIS, H. H., 1974. – Genetic variation and population ecology of some Southeast Asian frogs of the genera *Bufo* and *Rana*. *Biochem. Genet.*, **12**: 121-145.

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